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JOURNAL OF ANATOMY

FACIAL MUSCLES

THE MODIOLUS AND MUSCLES SURROUNDING THE RIMA ORIS WITH SOME REMARKS ABOUT THE PANNICULUS ADIPOSUS[1]

By G. H. S. LIGHTOLLER

INTRODUCTION

The material for this article was obtained from the following sources:

1. The heads of two Australian aboriginals (H.B. 1 and D.B. 2). These have been and are being more fully dealt with in other papers by Dr Burkitt and Dr Lightoller.

2. The head of an European female. This was an elderly female (85 years) and a dissecting room subject in the Anatomy Department of the University of Sydney, No. 2317.

3. The head of an European male, aged 104 years, also a dissecting room subject in the Anatomy Department of the University of Sydney, No. 2325.

4. A foetal head supplied by the Anatomy Department of the University of Sydney. This foetus was of European parentage and of about eight months.

5. Sections of lips taken from

(*a*) Australian aboriginal D.B. 2.

(*b*) An European female, No. 2317.

(*c*) ,, foetus, 7/12ths old.

(*d*) ,, ,, 9/12ths old.

(*e*) A female chimpanzee.

All the sections were cut sagittally and were taken from an area just below the ala nasi. This was done in the hope of obtaining the fibres of the M. quadratus labii superioris in longitudinal section and was fairly successful.

In the lower lip, owing to the marked obliquity of the M. quadratus labii inferioris and portio labialis platysmae, the fibres were cut transversely and the consequent picture was much less clear.

6. An European female, aged 35 years, who was the subject of the rare disease Lipodystrophia progressiva. In her case the lower limbs as far as the iliac crests were perfectly normal and there was no great increase of adipose tissue. The rest of the body was almost devoid of any panniculus adiposus and showed very clearly the action of the muscles. Slow-moving pictures (one-quarter the usual rate) were taken of her face whilst she performed various movements, and the films were then examined with an orthoscope.

7. Master O. A., aged 8 years, of European parentage, in whom was severed

A note concerning the publication of this paper is given on page 85.

at operation the cranial branch of the 7th cranial nerve, thus paralysing a portion if not the whole of his platysma on that side.

No attempt has been made in this article to describe completely the muscles concerned. Where the origin or the insertion has been fully dealt with in text-books, no further mention has been made about them, but slight rearrangement of the musculature has been suggested, and in addition, fuller detail given with regard to some of the insertions and some of the origins.

It is surprising that some of the anatomical facts have not hitherto gained acceptance in English text-books, e.g. the portion of the platysma called in this article the portio labialis platysmae, was described and figured by Henle in 1871 (11) and the anatomical facts about the M. mentalis were described and figured by Virchow in 1908 (31).

For convenience of reference a number of tables or lists have been added.

Table F contains a number of statements with regard to the muscular activity which are in reality the result of observations upon the living face that was cinematographed, but as they have formed the basis of the descriptions, it was thought advisable to put them into a short and separate table.

Owing to the fact that the facial muscles are described for the first time as actually seen in action, the current anatomical terminology has been increased by a few new terms. Definitions of these are given here for the convenience of the reader.

LIST OF DEFINITIONS

Antimere (10). A part symmetrical with or corresponding to a part in the opposite side of the main axis (Funk and Wagnall).

Basis modioli is that area of the mucous membrane lying beneath the modiolus and to which are attached portions of the various muscles of which the modiolus is composed. Medially, superiorly and inferiorly the margins are clearly marked but laterally there is drawn an imaginary line vertically beneath the sharp edge of the modiolus.

Dominant, as applied to muscles, means that a muscle or group of muscles at that moment is the chief or controlling factor in its own group.

Labial cords means the formation of the lips into musical stops similar in function to the vocal cords.

Labial tractor is the term applied to the M. quadratus labii superioris and (or) the M. quadratus labii inferioris and the portio labialis platysmae when speaking of them as antimeres to the M. orbicularis oris.

Modiolus (Latin modiolus—nave of a wheel) is the name applied to the muscle mass at the corner of the mouth called by the Germans "der Knoten."

Paramere. The former definition of the term antimere is corrected by terming each ray a paramere and its symmetrical half an antimere.

Resistant. As applied to muscles, means that a muscle or group of muscles at that moment is the lesser or balancing factor in its own group (i.e. it is being stretched by its antimere and to this process it offers an active (contractile) or passive (elastic) resistance.

M. MALARIS

(*Pars peripheralis, M. orbicularis oculi*)

In the dissection of the Australian aboriginal the most striking feature is the apparent absence of differentiation of the facial muscles lying in the oculo-bucco-labial region.

This has also been observed by others in the American negro, South Sea Islander (17), etc. On closer observation, however, it was found that this lack of differentiation was not actually the case but rather that the facial muscles (M. zygomaticus, M. quadratus labii superioris) which one is accustomed to see in this region in the European, have been overlaid and concealed by a large sheet of fibres continuous with and probably forming part of the M. orbicularis oculi.

This sheet is more or less attached to the subjacent muscles, though the caput infraorbitale, M. quadratus labii superioris, is less involved than the others. This is the M. malaris, discovered and figured by Henle (11). The muscle consists of two portions, a lateral and a median (caput laterale and caput mediale). The caput laterale is contiguous with and has a similar origin to the pars orbitalis, M. orbicularis oculi, from the temporal fascia.

Of variable extent according to race and individual the fibres proceed obliquely downwards, forwards and medially.

In the Australian aboriginal these fibres cover completely the M. zygomaticus and caput zygomaticum, M. quadratus labii superioris, and stream downwards to the upper lip. The outer third of the upper lip is completely ensheathed with these fibres which cover and entirely hide the pars peripheralis, M. orbicularis oris (Table C, 35 and 36).

At its lateral edge this muscle is directly continuous with and inseparable from the M. zygomaticus, though a portion of this latter muscle may be quite distinct from the M. malaris. Also some of the most lateral fibres of the M. malaris accompany the M. zygomaticus towards the modiolus and some also seem to pass into the caput latum or caput buccale M. triangularis. Occasional fibres pass directly into the superficial fascia of the cheek.

In the European female No. 2317 (Table C, 41) there was an extremely well-developed caput laterale. Its origin was as described above though not so extensive and it completely hid from view the M. zygomaticus and the caput zygomaticum. There was no union or interlacement of fibres between the caput laterale and the deeper lying muscles. Its fibres, however, did not reach as far as the lip but ended in the fat of the cheek and the nasobuccal gyrus (Table C, 41). Both in the cheek and gyrus they were overlapped by the caput mediale as they lay behind or deep to these fibres.

Caput mediale. This was better developed in the Australian aboriginal and these findings will first be described. The medial fibres were continuous with the M. orbicularis oculi and took origin from the medial palpebral ligament and the nasal process of the maxilla. These fibres covered completely and hid from view the caput angulare, M. quadratus labii superioris, which was separated from it by a small layer of fatty tissue. These fibres all streamed obliquely downwards, forwards and laterally to cover the medial area of the upper lip in a manner similar to the caput laterale in the lateral third of the upper lip. The more lateral fibres of the caput mediale took origin from the nasal process of the maxilla between the medial fibres and the M. orbicularis

oculi, and gained little attachment to the medial palpebral ligament. Their origin was apparently deeper than these neighbouring muscle bundles.

These fibres streamed in a more or less definite bundle laterally and slightly downwards, lying beneath the nasobuccal gyrus and was previously called the M. oculobuccalis (4). Its fibres were inserted into the fatty tissue in the lateral and lower end of the nasobuccal gyrus, crossing anterior to the caput laterale.

In the European female No. 2317, the caput mediale was remarkably well developed, also, though no differentiation could be distinguished in the mode of origin of the medial and more lateral fibres. The origin was continuous with the M. orbicularis oculi and was from the medial palpebral ligament and the nasal process of the maxilla.

The caput mediale M. malaris lay anterior to the caput angulare M. quadratus labii superioris and completely hid the cranial portion of this muscle from view. It was separated from it by a wedge of fatty tissue.

The fibres of the caput mediale proceeded from their origin downwards and laterally spreading themselves meanwhile like the rays of a fan and gained insertion into the panniculus adiposus of the nasobuccal gyrus. It lay anterior to, and to some extent crossed the fibres of the caput laterale.

In the European male No. 2325, both capita laterale and mediale were clearly demonstrable and occupied much the same position and relations as already described (Table C, 44).

In the European foetus there was a very well-developed M. malaris, both heads being astonishingly muscular (Table C, 45).

In the primitive condition of this muscle as is seen in the Australian aboriginal, the caput laterale M. malaris would naturally be called into play during laughter to raise the upper lip and corner of the mouth as a coadjutor to the M. zygomaticus. But its very activity would also necessarily cause the well-known wrinkling at the outer corners of the eyes, which is such a well-recognised feature of laughter.

In the European this synchronous activity probably persists in spite of the fact that the muscle fibres seldom reach as far as the lip. Fibres reaching the lip are, however, described by Henle (11).

Both these sets of fibres have been accurately described and figured in more primitive or in coloured people. (J. J. Koster in the Sunday Islander (17), F. Kudo in the Japanese (18).) These fibres are described as belonging to the M. orbicularis oculi. With the absence of material from primitive people or even highly civilised and cultivated people like the Japanese, on whom these fibres are exceptionally developed, it was only natural that the text-books should consider these fibres to be some of the many fibres which end blindly in the panniculus adiposus of the cheek.

But when one considers these heads and afterwards dissects for this sheet in European heads they are found to correspond to a large extent and the only point of divergence is the failure to reach the lips.

One interesting fact with regard to the caput mediale may be mentioned here, namely, that in some heads the caput mediale can be seen to form part of the same muscular sheet as the depressor capitis supercilii, e.g. in the Australian aboriginal D.B. 2 and possibly in (17) and (18).

Ruge ((28), p. 285) in his description of the lemurs, describes and figures in Lepilemur and Chiromys a very full development of the M. auriculo-labialis which he divides into three portions: (1) Auriculo-labialis proprius; (2) Temporo-labialis; (3) Orbiculo-labialis.

The orbiculo-labialis portions are very closely adjacent to the circular fibres of the M. orbicularis oculi.

He also states that the portion of the circular fibres found in the lower lid are derived from aberrant fibres of this orbiculo-labialis portion of the M. auriculo labialis.

The caput lateralis M. malaris must therefore represent the survival or "rest" of this orbiculo-labialis portion and it seems to be very commonly present and is well-marked in the foetus.

With regard to the caput mediale it also is a survival or "rest" of a much more primitive musculature. Huber ((13), p. 305 *et seq.*) shows that the M. procerus nasi is a "rest" of the auriculo-orbito-nasal musculature and further that it is the representative of this above the eyes ("Supraorbital-naso-labialis") and before the "infraorbital"-naso-labialis has been split off. He also shows that the M. procerus nasi can cover not only the bridge of the nose but can spread out laterally and reach not only the ala nasi but even the upper lip. Further, he shows that the M. depressor capitis supercilii is probably derived from the same sheet of primitive auriculo-orbito-nasal musculature.

The caput mediale must be taken to represent the survival or "rest" of the same primitive musculature but unlike the above-mentioned examples it is commonly present and is well marked in the foetus.

M. NASALIS

In dealing with this muscle it is taken to consist of only two portions—the pars alaris and the pars transversa. Concerning the depressor septi there seems to be much ambiguity, as Cunningham and Spalteholz call by this name the median fibres of the pars alaris which undoubtedly have insertion into the septum nasi mobile. However, Eisler and McMurrich will be followed in this article and they treat the pars alaris as having both septal and alar insertions, but call by the name of the depressor septi the M. naso labialis.

The name of pars nasalis M. orbicularis oris previously given by F. Arnold has been retained as being more in keeping with the rest of the nomenclature. This pars nasalis M. orbicularis oris when present, almost completely hides from view the pars alaris M. nasalis. It may, however, be absent and in this case the cephalad fibres of the pars alaris are easily seen.

The *pars transversa* has previously been described (4) as forming "a nearly complete constrictor of the nose aperture not at the nostril, but laterally at

the junction between the vestibule and the true nose cavity." This action is extremely well exemplified in the pronunciation of the consonantal sounds, especially "P" and "B" and well seen in the crying new-born infant.

A fair idea of this is gained by comparing Table C, 6 (*a*) and (*b*). Even here it is not nearly so convincing as in the moving picture itself, when one sees at the completion of the sounds the almost dramatic springing back of the ala nasi and the portion of the nose immediately posterior to it. This compression of which may be called the post vestibular area of the nose by the pars transversa M. nasalis of necessity must compress the posterior portion of the ala nasi thus bringing about a narrowing of the anterior nares.

This narrowing of the anterior nares is often helped by the action of the median labial fibres of the caput angulare M. quadratus labii superioris as they curl around the ala to gain insertion into the lip close to the philtrum.

The effect of this activity of the pars transversa M. nasalis is to block more or less effectively the nostril and so assist in maintaining the air pressure within the cavum oris.

Pars alaris. The activity of this portion of the muscles is of necessity difficult to demonstrate, but if we compare Table C, 10 (*a*) with 13 (*d*) there appears to be much less sharp definition of the ala nasi from the upper lip in the two latter cases and in Table C, 13 (*b*) there almost seems to be a definite ridge caused by the action of the pars alaris.

This ridge or lack of definition of the ala is due to the activity of the pars alaris dragging the ala outwards and slightly downwards, the muscle being thus a partial antimere to the nasal portion of the caput angulare M. quadratus labii superioris.

With the caput angulare pulling the ala nasi cranially and the pars alaris M. nasalis pulling caudally and laterally the ala nasi, and caudally the inferior border of the nasal opening and septum mobile we can see that the triangular exterior nares is very considerably modified in shape and made to approach the circular. This gives, of course, the greatest possible aperture.

From the above it follows that to increase the capacity of the nasal airway there is primarily a widening of the anterior nares and secondarily a widening of the post vestibular area. To decrease the capacity of the nasal airway there is a primary narrowing of the post vestibular area and a secondary narrowing of the external nares.

Depression of the nasal septum if it have any effect at all would rather be to widen the airway.

With regard to the derivation of the M. nasalis, Huber, in a private letter, states that it is derived from the M. canino-orbicularis (oris) and that the pars transversa must not be considered to be derived from the M. naso-labialis (or the caput angulare M. quadratus labii superioris). As the preceding description of the M. nasalis has suggested another possible origin of the muscle, based on its physiological action, and as there is at present great difficulty in deciding from whence it is sprung, the following suggestion is given, though with

diffidence, as it is outside the scope of the present article. It is suggested that the pars transversa has probably been derived from the M. orbicularis oris superioris or the canino-orbicularis (Huber) in much the same fashion as the M. mentalis is derived from the M. orbicularis oris inferioris. This is confirmed to some slight extent by the fact that the pars transversa is called into action at the same time as the M. orbicularis oris and that the more vigorously the latter acts, the more marked is the action of the former.

We shall see that the true antimere of the M. orbicularis oris is the M. quadratus labii superioris. Also the pars alaris is antagonistic to the pars transversa and they do not act simultaneously.

Therefore, it is improbable that they are both derived from a common stock but must have probably been derived from antimeres. Now the pars alaris acts in conjunction with and at the same time as the caput angulare M. quadratus labii superioris, or at least, as the nasal portion of that caput. Again, the central fibres of the caput angulare curl around the ala nasi to gain insertion into the upper lip as far down as the red lip margin. Also, the deepest or most posterior of these fibres turn directly backwards and are inserted into the mucous membrane of the upper lip.

It is suggested that the caput angulare was originally a much wider sheet of muscle and proceeded to the primitive ala and gained insertion into the medial end of the maxillary process. Then the eyes become less lateral in position and the primitive alae expand laterally dividing the medial fibres into two separate muscles, the one above and the other below, the nasal opening. Then Table F, 7 came into play causing a great increase in the distal portion of the muscle and giving us the pars alaris M. nasalis as we see it in the adult.

On this assumption the M. orbicularis oris and the pars transversa M. nasalis would have been on a deeper plane than the pars alaris. All these superficial fibres have disappeared and we have only the nasal portion of the caput angulare M. quadratus labii superioris lying superficial to the pars transversa M. nasalis to indicate their original relations.

M. QUADRATUS LABII SUPERIORIS

(Table C, 16, 22, 25, 33, 34, 41, 44)

The following is a description of this composite muscle as found in the dissection of a head of an European female in the Anatomy Department of the University of Sydney, Medical School, No. 2317.

Caput angulare. This lay on a slightly deeper plane than, and was separated by some fatty tissue from, the caput mediale M. malaris. It ran downwards and slightly anteriorly towards the superior end of the nasolabial fold where it turned towards the nose wing and was inserted as follows:

(*a*) Here the lateral fibres of the muscle lay directly anterior to, and crossed at an angle, the other two heads of the M. quadratus labii superioris.

All these fibres were inserted *en echelon* into the nasolabial fold. Their function would appear to be to raise this fold and in so doing would cause the

transverse wrinkles across the root of the nose. If the action of the head were rapid one could have a fine tremor of the upper end of the nasolabial fold, as was seen when the emotion of contempt was enacted for the cinema.

(*b*) The fibres just medial to these lateral fibres join themselves to the medial edge of the fibres from the caput infraorbitale and curling around the alae nasi proceed downwards and forwards as far as the red lip margin. The more exact insertion of these fibres will be considered later, but it may be stated here that, though these reach to, they do not appear to penetrate into the philtrum.

(*c*) The most medial fibres proceed downwards and forwards to gain insertion into the cephalad end of the ala nasi which it tends to raise.

Caput zygomaticum. This, the smallest of the three heads, sends some of its most superficial fibres to gain insertion into the skin and superficial fascia of the nasobuccal gyrus. The remainder of the muscle joins itself to the lateral margin of the caput infraorbitale and proceeds with it into the lip. Overlying the head and concealing much of it were the fibres of the caput laterale M. malaris. These also end in the nasobuccal gyrus at a plane deeper than the caput mediale, but they are quite separate from the fibres of the caput zygomaticum, which enter the gyrus.

Caput infraorbitale. The largest of the three heads, it seems to be distributed entirely to the lip where it spreads out fanwise into a sheet parallel to and immediately subjacent to the skin. The following description of the insertion of this muscle will be considered as including with it the accession of fibres it gains from the other two heads and will be based on microscopic sections as well as the macroscopic dissection.

The most superficial of these fibres was easily demonstrable in this European by shaving instead of dissecting the skin from off the upper lip. Fine thicknesses of skin were successively shaved off until at last muscular fibres were easily discovered in amongst the hair follicles and sebaceous glands, though no unbroken sheet of fibres could be demonstrated such as was seen in the heads of the Australian aboriginal. It was also noticed in the Australian aboriginal that this sheet of fibres was very much thinner at the red lip margin than just below the naso-labial fold. Occasionally, in the living subject, there is to be seen a distinct linear ridge or dimpling below the naso-labial fold, though not parallel to it. This was noticed when the subject was talking and laughing and was apparently caused by the insertion into the skin of the upper lip, of the first line of fibres of the M. quadratus superioris. Fortunately, this does not often show as it certainly did not improve the looks of the women, in whom it was evident.

This sheet of muscle fibres apparently did not cross into the philtrum, though they reached near to its lateral margin. Laterally, they apparently extended out only as far as the red lip area. Whether it is universally true that the lateral distribution of the M. quadratus labii superioris corresponds with the ending of the everted red of the lip at present cannot be stated, but it

apparently was so in the cases dissected. Next sections were made of both lips immediately below the outer edge of the external nares. It was then seen that the muscular sheet entered the lip near its middle and close to the pars peripheralis M. orbicularis oris. It then split into two or three sets of fibres, the deepest remaining in close contact with the pars peripheralis M. orbicularis oris and the two superficial sets running obliquely forwards to reach the corium about 5 mm. above the red lip margin. Here they formed a sheet curved convexly forwards, and ultimately the deeper fibres turned abruptly backwards towards the mucous membrane of the lip. Considered in detail the three different sets of fibres were:

(*a*) The most superficial fibres were inserted *en echelon* into the corium of the skin amongst the hair follicles and sebaceous glands of the upper lip as far as the red lip margin.

The fibres were very short and would not be described separately, were it not for the fact that apparently they do not always act with the same vigour as the other portions (*vide* labial tractor).

(*b*) Immediately below this and forming part of the same group of fibres were a well-developed set of fibres which proceeded immediately beneath and parallel to them. But before reaching the red lip margin these fibres turned backwards and downwards, insinuating themselves between the pars marginalis and pars peripheralis of the M. orbicularis oris to gain insertion into the corium of the mucous membrane beneath the posterior portion of the red lip area and into the red lip area itself (Table C, 1 (*b*), (*c*), (*d*), and 33).

(*c*) Higher up in the lip a deeper set of fibres detached themselves off from the above more superficial ones and became separated from them by a thin wedge of fibrous tissue. These fibres remain closely attached to the pars peripheralis M. orbicularis oris which they, from time to time, penetrate to be inserted into the corium of the mucous membrane of the lip. They also seemed to be either attached to or passing close and deep to the labial glands. The action of these fibres must be to lift both glands and fibrous tissue upwards and towards the pars peripheralis M. orbicularis oris and away from the lip margin. Often in the living subject one can see a deep groove on the posterior aspect of the lip near the junction of mucous membrane and red lip. This is due to the action of fibres (*b*) and (*c*). In the upper lips (and also the lower) of the Australian aboriginal, European foetus and of a female chimpanzee, somewhat similar conditions were observed. But in the two latter, there did not seem to be any division between the (*b*) and (*c*) fibres.

All three heads are illustrated in Table C, 14 (*c*) and it will be seen that both the angular and infraorbital heads gain attachment to the red lip margin. Strangely enough, the M. quadratus labii superioris shows but three well-marked points of attachment in Table C, 14 (*c*), which at first sight might be

thought to be abnormal and peculiar. This, however, is not the case for the muscle has a continuous series of muscular tendinous insertions into the skin immediately above the red lip area, as is shown in the diagrams. We get this shown, indefinitely it is true, in saying letters like "P" and "B," and also in the evenness of the lip movement in Table C, 13 (*a*), (*b*), (*c*), (*d*), and in C, 14 (*a*). Then an inspection of the M. zygomaticus in Table C, 14 (*c*) shows that it, too, is represented by a sharply marked single thread-like muscle belly very similar in every way to those of the M. quadratus labii superioris (cf. Table C, 14 (*c*) and 12 (*d*)). The explanation is first of all in the unexpected amount of muscular exertion and strain that is required for this movement of the upper lip.

Secondly, there must be a certain amount of twist in the muscle bellies and hence the outer margin of the infraorbital head and the medial and lateral margins of the angular heads are the ones on which most strain would fall.

The caput zygomaticum is well shown here in Table C, 14 (*c*), but it is equally well seen in the letters, "B," "P," etc.

In Table C, 13 (*a*) one sees the appearance of the moderate action of the whole muscle; here the upper portion of the naso-labial fold is quite obliterated by the wedge-shaped muscle mass proceeding at right angles across it.

The Y-shaped upper portion of the mass shows the origin of the two main heads. No strands or ridges show as yet in the upper lip, though the formation of labial cords is well developed.

Caput angulare. In Table C, 13 (*c*) the M. quadratus labii superioris depicted as resistant to the dominant orbicularis oris, and the angular head, is taking a more active part than either of the other heads, for it is the very centre of the lips which are so actively engaged in forming the consonant sound "P." This enables us to see very clearly the strong muscular belly passing round the ala nasi and then turning downwards close to the philtrum.

Other pictures, e.g. Table C, 14 (*c*), show us this as two ridges which extend across the upper lip as far as the red lip margin.

In Table C, 13 (*b*) we also see very distinctly one small band of muscle inserted into the ala nasi in its upper and external surface thus pulling the ala nasi upwards and widening the nostril. This has been referred to when speaking of the M. nasalis.

There is also very plainly seen in the upper lip, the two ridges caused by the angular and the one by the infraorbital head.

Notice also at the root of the nose, the oblique ridges caused by the action of the caput angulare, Table C, 13 (*b*), (*d*).

These occur at some distance from the point of insertion of the caput angulare into the naso-labial fold. This is due to the nasobuccal gyrus and its firmly adherent skin being moved upwards against the less dense panniculus adiposus with its somewhat more loosely attached skin.

Table C, 13 (*b*) also shows the result of the action of the three heads of the M. quadratus labii superioris upon the face. The lower end of the philtrum is

drawn up with a well-marked crescent, and there is a tendency for the outer third of the upper lip to be slightly drawn up also. (This will be seen much better in Table C, 13 (*d*), and 14 (*a*).) The ala nasi is drawn slightly upwards, the bridge of the nose is scored with lines approximately at right angles to the direction of the muscle and the naso-labial fold is deepened and drawn slightly upwards and slightly outwards.

Caput zygomaticum. The solitary action of this head is not seen. In Table C, 14 (*a*) (contempt) the M. quadratus labii superioris is dominant and the M. orbicularis oris feebly resistant and the naso-labial fold is again deepened and drawn upwards and slightly outwards. The muscular belly is visible above this. The ala nasi is not affected but the canine sneer is very noticeable and this is due directly to the infraorbital and zygomatic heads. During the expression of this emotion of contempt one very striking movement occurred in the living subject which is not seen well, if at all, in the cinema. It must be remembered that the cinema shows the movements of the face at quarter the normal rate and so movements that were small but rapid enough to strike one's attention, may be wholly missed upon the screen.

The movement alluded to was the very rapid up and down trembling of the upper portion of the naso-labial fold reminding one most forcibly of the fine movements seen in the quivering nostril of a mouse. This was most probably due to the rapid action of the caput angulare.

Beyond being able to demonstrate the presence of the caput zygomaticum in various slides (e.g. Table C, 13 (*c*), and 14 (*c*)) no other information has been gleaned as to its action. It would seem, however, to make more vertical the pull of the caput infraorbitale upon the outer third of the red lip area.

Besides the effect of the M. quadratus labii superioris upon the shape and position of the upper lip, and the direct effect of the caput angulare upon the naso-labial sulcus, the muscle may indirectly affect and alter the curvature of the latter.

The upper lip is anteriorly a solid muscular organ with no fat and little, if any, fibrous tissue intervening between the muscle and the skin. Moreover, the muscle lies amidst the papillae of the hair follicles.

When this muscle mass is moved upwards there is a tendency to pull it underneath the fatty nasobuccal gyrus and, in so doing, it will alter the curvature of the naso-labial furrow.

Caput infraorbitale. The action of the caput infraorbitale is well seen in Table C, 13 (*b*), 13 (*d*) and in 14 (*a*), which has already been described. It drags cephalad the lateral portion of the upper lip in which action it is assisted by the caput zygomaticum.

M. QUADRATUS LABII INFERIORIS
(Table C, 16, 26)

The superficial fibres of this muscle always appear to be very pale, i.e. the fibres proceeding to the skin and lying in the mass of fatty and fibrous tissue

of this area. The rest of the muscle is normal in colour. This muscle arises from the tuberculum mentale immediately above the insertion of the caput longum M. triangularis and for a distance laterally of 2–2·5 cm. along the outer surface of the lower border of the mandible.

In this latter part of its course it is in juxtaposition to part of the insertion of the portio mandibularis platysmae and occasional fibres seem to pass between the two muscles.

Diagram C, 27 demonstrates the presence of two bare areas in the anterior part of the mandible:

(*a*) Between and inferior to the origins of the two heads of the M. mentalis. This is for the sub-mentalis bursa.

(*b*) Between the origin of the M. incisivus inferioris and the foramen mentale and the lower border of the mandible and the gingira.

The M. quadratus labii inferioris and portio labialis platysmae together form a strong muscular sheet comparable in its action and similar in its mode of insertion to the M. quadratus labii superioris. They are, in fact, the labial tractors of the lower lip. In cross-section, if the muscles are separated, we notice both the muscles to be triangular in outline, the portio labialis platysmae having its base near the mouth angle and its apex medial and the M. quadratus labii inferioris with its base medial and its apex towards the mouth angle.

A few mm. of the lateral portion of this muscle are covered superficially by the portio labialis platysmae and it is the fibres of this latter muscle which alone, as far as can be ascertained, reach the skin and the red lip margin in this lateral region. More medially, however, the M. quadratus labii inferioris projects beyond the free margin of the portio labialis platysmae and here it reaches the skin and red lip margin. It also decussates in the middle line with its fellow of the opposite side to a greater or less degree according to the race and individual peculiarities.

It may be mentioned here that the M. quadratus labii superioris and the M. quadratus labii inferioris and portio labialis platysmae will, for the sake of brevity and clearness, often be spoken of as the "labial tractors."

Originally the portio labialis and portio mandibularis platysmae and the M. quadratus inferioris formed part of the main platysmal sheet, the portio labialis forming the superficial and the portio mandibularis and the M. quadratus labii inferioris the deep layer. But when the deep layer became attached to the lower jaw, the neck portion remained the same, but the lip portion, i.e. the M. quadratus labii inferioris, developed greatly and became a much more powerful sheet of muscle ((27), p. 474).

In all probability the size of the portio mandibularis will bear no relation to the other two muscles. But the size of the M. quadratus labii inferioris will probably vary inversely as the size of the portio labialis platysmae.

Insertion of the inferior labial tractors. The insertion of the M. quadratus labii superioris has been described in detail, so it is a very easy matter to understand from this the insertion of inferior labial tractors and their action.

Briefly, it may be stated that there are three groups of fibres:

(*a*) The most superficial which are inserted *en echelon* into the corium of the skin almost as far as the red lip.

(*b*) Fibres immediately beneath (*a*) and really forming part of the same sheet. These do not reach the skin but a little above the red lip turn abruptly upwards and backwards between the pars marginalis and pars peripheralis orbicularis oris to be inserted into the corium of mucous membrane of the red lip area.

(*c*) A deeper set of fibres more or less separated from (*a*) and (*b*) which decussates with and penetrates through the fibres of the M. orbicularis oris to be inserted into the corium of the mucous membrane of the lip and also into or around the capsules of the labial glands.

At the basis mandibulae the portio labialis platysmae overlaps by a few mm. only, the fibres of the M. quadratus labii inferioris. But the fibres of the two muscles are not always quite parallel, the portio labialis platysmae occasionally running more horizontally and the M. quadratus labii inferioris more vertically.

When this is the case, it greatly facilitates the separation of the two muscles in dissecting. But it is by no means always so, as was well illustrated in No. 2325. There the fibres of both muscles were indistinguishable on surface examination. Moreover, a thin sheet of M. quadratus labii inferioris fibres arose from the bone under the whole breadth of the portio labialis platysmae and were inseparable from this. The furthest lateral extent of this was 4 cm. from the mental tubercle.

These fibres would not, of course, reach the skin but would form the (*b*) or (*c*) fibres of the labial tractors.

It follows, therefore, that as we approach the lip, the portio labialis platysmae overlaps in an ever increasing amount the M. quadratus labii inferioris. This has a very definite bearing upon the final insertions of these two muscles.

Nearest the angle of the mouth the portio labialis platysmae will possess (*a*), (*b*) and (*c*) fibres. Nearest the middle line the M. quadratus labii inferioris will possess (*a*), (*b*) and (*c*) fibres. In the intermediate area the portio labialis platysmae will lose first its (*c*) fibres, then its (*b*) fibres and the fibres from the M. quadratus labii inferioris will take their place until finally it replaces the muscle altogether.

PLATYSMA

(Table C, 17, 43, 44, 45)

Bluntschli ((2), p. 241) divided the platysma of the neck into two main portions, the pars aberrans and the pars labialis and this classification has been kept. In this article only the pars labialis will be considered. In the dissection, this part of the platysma fell naturally into three parts:

(*a*) *Portio modiolaris* consisted of those fibres (some of which pass deep to the caput buccale M. triangularis) which gain insertion into the modiolus.

In the absence of the caput buccale M. triangularis it would be fibres from this portion of the platysma which would take up its action and might have been classed as M. risorius.

(*b*) *Portio labialis* (portio labialis proprius). By dissecting up the fascia covering the platysma it was found that at the same time was raised the caput latum M. triangularis. Then by cutting transversely through the caput longum M. triangularis the continuity of platysma fibres as far as the red lip margin was easily demonstrated.

The portio labialis platysmae is formed by those fibres of the platysma which pass beneath the free posterior border of the caput longum M. triangularis and thus proceed beneath the muscle without interruption and emerge from beneath its free anterior edge. All its fibres therefore lie superior to the origin of the caput longum M. triangularis. Those fibres which interdigitate with the fibres of origin of the caput longum M. triangularis, are so few in number and so feeble that they serve rather to indicate the original connection between the M. quadratus labii inferioris and the platysma than any useful physiological function. It would, therefore, seem that the size of the portio labialis platysmae would vary as the amount of origin of the caput longum M. triangularis from the basis mandibulae lateral to the tuberculum mentale.

In the heads, Nos. 2317 and 2325, this was to some extent true, but the difference was not so marked as was expected owing to the direction of the platysma fibres. In No. 2317 the platysma fibres as they approached the mouth became more horizontal in direction. In No. 2325 the fibres in this position were much more vertical in direction.

This was the more surprising as No. 2325 had a well-marked nape platysma which was not present in No. 2317. In both cases the neck platysma consisted of a pars aberrans and a pars labialis.

The portio labialis platysmae is inserted into mucous membranes and the red lip as well as the skin of the lower lip in the manner described for the M. quadratus labii superioris. This insertion is, however, only limited to the middle portion of the lip for the mesial portion of the lip is occupied by the M. quadratus labii inferioris insertion and the lateral portion or that portion nearest the angle of the mouth has no labial tractor inserted into it.

(*c*) *Portio mandibularis* consists of those platysma fibres which gain attachment to the mandible. They include fibres which lie deep to the portio labialis platysmae as well as the more mesial fibres. The insertion of this muscle is, as a rule, much more extensive than is expected. It is seldom that its median fibres do not meet and more often decussate with its fellow of the opposite side just below the chin.

In these cases it gains an insertion into the basis mandibulae immediately below the base of the protuberantia mentalis. Should the caput longum M. triangularis have an extensive origin also from this area, there is an intimate intermingling of the fibres of both muscles.

If, however, the origin of the caput longum M. triangularis should not be

so extensive and in its stead there exists a M. transversus menti, then the platysma takes its origin immediately beneath the fibres of this muscle.

LABIAL TRACTORS

The action of the labial tractors as illustrated by the portio labialis platysmae

Apart from the dissection just described, a very instructive method offered itself for examining the action of this portion of the muscle. This was in the case of a small boy in whom this portion of the platysma was paralysed without any affection of the other facial muscles. A cinematographic record (taken at the ordinary speed) was made of the condition. He had been operated upon for enlarged cervical tubercular glands in the left side of the neck and the surgeon was unable to save a small nerve (Table C, 1 (*a*)). This was evidently the cervical branch or branches of the 7th cranial nerve and resulted in the paralysis of the portio labialis platysmae and probably also of the portio mandibularis platysmae. This latter caused no symptoms and perhaps for a like reason the portio modiolaris platysmae could not be excluded from involvement.

The paralysis of the portio labialis platysmae, however, caused marked symptoms which fully bore out the anatomy of the muscle as recently described. These symptoms were noticed as soon as the patient recovered from the anaesthetic (Table C, 1 (*a*), (*b*), (*c*), (*d*)).

(1) When the face was quite at rest the symptoms were not very marked and might quite easily have been overlooked. There was then only a slight fulness of the red lip surface on the left side of the lower lip; this became exaggerated if the child were tired.

(2) When the child smiled, one noticed a definite flattening of the upper red lip surface of the right side of the lower lip accompanied by a pitting and puckering of this surface as though it were being pulled downwards. On the left or injured side, no puckering or pitting of the red lip but the fulness alluded to above, remained unaltered.

(3) In full laughter not only did this flattening and puckering persist on the right side but in addition the whole of the lower lip was bowed downwards upon this side into a true arch or curve and exposing the teeth upon this side. Upon the left side, however, the fulness of the red lip persists and the whole of this side of the lip is pulled upwards in a straight line and the teeth are not exposed.

But we must exclude from this description the central quarter of the lip for this is not involved in the paralysis. This fact deserves special mention as it exemplifies still more fully the anatomy of this region, showing that the M. quadratus labii inferioris is not paralysed.

Here we notice that even on the paralysed side the medial eighth of the lip is pulled downwards equally with the medial eighth of the unaffected side. This activity must be due to the M. quadratus labii inferioris which is not affected. This, of course, was to be expected as the nerve twig supplying the

M. quadratus labii inferioris does not come from the cervical loop of vii but from the ramus mandibulae of vii (10).

This observed activity can be translated into the terms already employed to denote the insertion of a labial tractor, viz. the (*a*), (*b*) and (*c*) fibres.

We notice that even when at rest the paralysis of the muscle showed itself by the fulness or lack of flattening of the affected side of the lip due to the lack of activity of the (*b*) and (*c*) sets of fibres. There was an exaggeration of this both in smiling and laughter.

But in smiling, and especially in laughter, there was in addition a complete failure to bow downwards the lower lip, no dimpling of the skin surface of the lip and no defining of the pars peripheralis M. orbicularis oris due to a firmly contracted sheet of muscle being stretched across it. This is undoubtedly an indication of the paralysis of the (*a*) set of fibres also as all of these features are clearly visible upon the right or unaffected side.

Part of the action of the portio labialis platysmae is therefore to pull the lower lip downwards, thus making a definite bow. Its antimere is the M. orbicularis oris. Thus the medial portion of the lip being pulled down to a greater or less degree by the portio labialis platysmae and M. quadratus labii inferioris, the remainder or lateral portion of the lower lip is influenced solely by the amount of contraction of the M. orbicularis oris, and by the position assumed by the angle of the mouth, due to the pull of the modiolus.

If the portio labialis platysmae is dominant and the M. orbicularis oris resistant, we necessarily get a bowing of the lower lip. If the orbicularis oris is dominant and the portio labialis platysmae and M. quadratus labii inferioris resistant, we get the pursed lips such as are seen very markedly in whistling, or the labial cords as in "P" and "B," or just the normal mouth closure.

When dominant, the portio labialis platysmae shows as a series of oblique ridges below the angle of the mouth, meeting and crossing at right angles the fibres of the caput longum M. triangularis. These ridges completely obliterate all trace of the active fibres of the upper portion of the caput longum M. triangularis (Table C, 3 (*c*), 6 (*b*), (*c*) and (*d*)). In these cases the only evidence of the activity of the caput longum M. triangularis is to be seen near its origin from the region of the tuberculum mentale, where fibres can be seen in active contraction.

M. TRIANGULARIS

(Table C, 16, 35, 36, 41, 42, 43, 44, 45)

In the present article the M. triangularis will not be considered as a single muscle but to consist of two heads—a deeper head arising from bone, and a more superficial head, arising from the fasciae of the neck and cheek.

The former has been called the caput longum and will presently be described more fully. The superficial head consists in its most fully developed state, of a fan of muscle fibres radiating to the modiolus (Table C, 43). The most lateral fibres may extend as high as the M. zygomaticus and the most medial lie anterior to the caput longum fibres (Table C, 45). The fibres of this

fan are of very variable length and are seldom complete, and the greatest gap exists between the most superior fibres and the remainder of the fan. The most superior fibres consist of a few isolated muscle fibres and has usually been known as the M. risorius. In this article it will be called the caput buccale.

The inferior fibres usually retain some semblance of their original fan-shape and will be called the caput latum. Thus, like the M. quadratus labii superioris, the M. triangularis consists of three heads:

All three heads are inserted into the modiolus.

Caput longum. This head is the only part of the M. triangularis which takes origin from bone.

It arises with a powerful musculo-tendinous origin from the tuberculum mentale and from a variable extent of the basis mandibulae medial to this and below the protuberantia mentalis.

At times the origin from the basis mandibulae may extend from tuberculum to tuberculum and in this case there is a strong interlacement of fibres from the opposite sides of the face, giving an impression of the existence of a M. transversus menti (Table C, 35). In this case also there will probably be, in this area, an intermingling with the insertion fibres of the medial portion of the portio modiolaris platysmae. Sometimes, the caput longum has also a linear origin from the basis mandibulae lateral to the tuberculum mentale and immediately below the origin of the M. quadratus labii inferioris from the basis mandibulae between the insertion of the portio mandibularis platysmae and the origin of the M. quadratus labii inferioris.

The extent of this origin may be equal to that of the M. quadratus labii inferioris as far lateralward as a line drawn vertically through the first molar tooth ((10), p. 113).

These fibres may be entirely absent or may be represented by a few weak fibres some distance apart and underlying the caput latum if this is well-developed (No. 2325).

In the latter case they may be completely covered by the caput latum. When these fibres are well developed they may be mistaken for the medial fibres of the caput latum.

Compare this with Koster's description of one of his Japanese heads ((17), p. 562).

Caput latum. This is of very variable size, sometimes being well developed and extending as low as, or even beneath, the basis mandibulae. In these cases its breadth at the basis mandibulae may extend as far lateralward as a line drawn vertically through the first molar tooth, and this gives a very definitely triangular appearance to the muscle.

At other times the caput latum may consist of only a few short fibres which

lie lateral to the caput longum. In all cases there is no bony origin for the caput latum. Its fibres invariably take their origin from the strong fibrous fascia covering the platysma and for this reason in a dissection the platysma should never be "cleaned up" until after the origin of the caput latum has been assured. None of its fibres have been seen either to be continuous with or to interdigitate with the fibres of the platysma or the M. quadratus labii inferioris.

Anterior to the caput longum there are often to be seen some short fibres similar to the caput latum which take origin from the panniculus adiposus or the fascia covering the M. quadratus labii inferioris. But as the latter is so feeble as to be difficult to demonstrate and the former contains so much fibrous tissue, it was impossible to decide the exact site of origin (H. B. 1, No. 2325 and foetal head, Table C, 36 and 45). These fibres have been described by Eisler and others ((10), p. 115 and (11), p. 155). In connection with these fibres a point of some interest may be mentioned here.

As stated in the commencement of the description, the M. triangularis consists of two portions—a deeper muscle belly attached to bone and a more superficial fan-like sheet of muscle. Now, if the short fibres occurring anterior to the caput longum belong to this fan, it is only reasonable to suppose that a few of the fibres of this fan will intermingle with the superficial fibres of the caput longum. If this be so, may not the M. transversus menti be merely a local powerful development of this fan, i.e. of the caput latum?

The caput latum will be taken to include the so-called transversus menti muscle which in future will be termed the caput transversum. In the few cases dissected in which this muscle was present it consisted of superficial fibres from the M. triangularis of the one side passing like a sling or loop under the chin to join the superficial fibres of the M. triangularis of the opposite side. In the part of its course beneath the protuberantia mentalis it occupies a position similar to the extended origin of the caput longum already mentioned, but is separated from the basis mandibulae by the median fibres of the platysma, which, beneath the cover of its fibres, gain attachment to the medial portion of the basis mandibulae. Thus the fibres of the so-called M. transversus menti pass direct from modiolus to modiolus and are not attached to bone or fascia in any part of their course. (See also under Modiolus, No. 2317, No. 2325 and Foetal head.)

Caput buccale. This third head of the M. triangularis is in reality the muscle usually known as the M. risorius.

Like the caput latum it is very variable in size. It takes origin from the fascia of the cheek either the strong fibrous tissue covering the platysma or even the parotid gland, or from the panniculus adiposus.

It may lie in any point of the compass between the caput latum which it may adjoin and the M. zygomaticus.

In connection with this it may be stated that in No. 2317 there was a well-developed caput longum and its insertion extended both medially and laterally to the tuberculum mentale, but there was only a rudimentary caput

latum and caput buccale. In point of fact, the capita latum and buccale were represented by a few sparse fibres, the one curling downwards and 6–8 mm. long and the other curling upwards and of a similar length. The caput latum fibres were from the fascia covering the platysma and the caput buccale from the surface of the corpus adiposum buccale. The function of the caput buccale was undertaken by fibres of the portio modiolaris platysmae which looked at first sight to be a true caput buccale though its fibres never crossed superior to a line drawn horizontally through the apex modioli (Table C, 41). This muscle was derived from the superficial superior fibres of the portio modiolaris platysmae which separated themselves from the main sheet and passed to the superficial portion of the modiolus covering the fibres of the caput longum.

Caudal to this the remainder of the fibres ran to their usual distribution.

On lifting this pseudo caput buccale, a rather unusual group of fibres was seen lying in the midst and evidently forming part of the deeper layer of the portio modiolaris platysmae. Two bundles of shorter fibres arose from the corpus adiposum buccale and proceeded with the platysma fibres to be inserted into the modiolus.

In No. 2325 (Table C, 43 and 44) there was a well-developed caput longum, but its insertion was confined entirely to the tuberculum mentale. The caput latum was well developed, containing fibres medial to the caput longum; lateral to the caput longum its fibres proceeded downwards across the basis mandibulae to the under surface of the neck extending almost across to the middle line. It formed a complete fan continuous with the caput buccale, which was fairly represented. The caput buccale lay partly above and partly below a horizontal line drawn through the centre of the modiolus. In this case, there was a true M. transversus menti (caput transversum).

In H.B. 1 (Table C, 35 and 36) there was a well-developed caput longum inserted into the tuberculum mentale and into the intertubercular area of the mandible lying below the protuberantia mentalis forming a pseudo transversus menti. There were in addition a few fibres of a true transversus menti (caput transversum).

The caput latum was feebly developed but contained fibres medial to the caput longum.

The caput buccale was feebly developed and lay in the horizontal line drawn through the modiolus.

There may therefore be described three types of M. triangularis:

(*a*) A well-developed caput longum whose origin does not extend lateral to the tuberculum mentale, and a well-developed capita latum and buccale.

(*b*) A well-developed caput longum whose origin does not extend lateral to the tuberculum mentale, but poorly developed capita latum and buccale.

(*c*) A well-developed caput longum whose origin extends widely lateral to the tuberculum mentale, but rudimentary capita latum and buccale.

Overlapping of these different types must occur.

The division of the M. triangularis into three capita has been adopted for many reasons:

(1) The muscle itself is variable as one may see by comparing the drawings in Spalteholz, Cunningham's *Manual of Anatomy*, 1918, or Morris's and Cunningham's *Text-books of Anatomy*. In the former, one sees the typical triangle shape represented clearly and sharply defined. In the last named, the muscle is by no means triangular and is represented chiefly by the caput longum of the present article.

In the two aboriginal heads dissected, we find the one showing the predominance of the caput longum and the other, the time-honoured triangle-shaped muscle.

(2) In the present article we see in the living subject in a way no dissection could demonstrate, how very sharply defined the caput longum is and how frequently it acts without support from the rest of the muscle. We also see here the same being true of the caput latum. This portion of the muscle (caput latum) can act in at least two sections, viz. a posterior and that portion of the muscle lying between this and the caput longum. This latter portion acts seldom and only for very brief periods, but the posterior portion acts very frequently, often by itself without the assistance of the remainder of the muscle and always sharply defined from the caput longum. In fact, it shows just as much individuality as the caput longum.

Some doubts may be expressed as to the visible swelling in the face described as due to the caput latum, being due to the muscle claimed, and it may be thought rather to be caused by the portio modiolaris platysmae.

Such, however, is not the case as can be very easily shown by comparing Table C, 8 (*b*), (*c*), or 14 (*c*) and 6 (*b*), (*c*), or (*d*).

It will be then seen that the swelling claimed to be due to the caput latum in Table C, 8 (*c*) is the same swelling as seen in Table C, 6 (*b*).

But in Table C, 6 (*b*) the portio labialis platysmae is acting with such force that its fibres can be seen extending as far laterally as the caput latum. This angle of incidence of these two muscles then makes it impossible for us to consider them as belonging to a common platysma sheet.

In Table C, 14 (*c*) where the confusion is greatest, it must be remembered that the modiolus has been dragged anteriorly thus making the swelling due to the caput latum appear more oblique than is usual.

(3) *Caput buccale.* This requires more consideration than either of the previous portions of this muscle as it is a big step to abolish the separate entity of a muscle which for so long has captured the imagination.

(*a*) But the M. risorius is not a muscle of laughter. This can be clearly and unequivocally demonstrated in the present article. It is a feeble but quite ordinary modiolar muscle frequently in use in speaking. It never acts alone but often assists other muscles to control the M. orbicularis oris. At times, in doing this, it seems to act as an antimere to the M. orbicularis oris instead of the M. buccinator, provided that the M. orbicularis oris is not acting too vigorously.

It apparently only acts if the modiolus is close to the neutral position. If the modiolus is definitely anterior the M. buccinator acts in its stead.

If the modiolus is definitely posterior the M. zygomaticus acts in its stead.

(*b*) Ruge in an older work(26) and Bluntschli ((2), p. 243) alone seem to suggest the possibility of the M. risorius being derived from the platysma. Ruge's work, unfortunately, is not available and Huber states in a private letter that he has since changed his opinion with regard to this. Bluntschli in a most interesting article classifies the different types of M. risorii but is not at all convincing when he tries to show the difference between the so-called platysma risorii and triangularis risorii. And even he confesses the triangularis risorii to be the common type and the platysma risorii in the nature of curiosities. All seem to take it for granted that the M. risorius is derived from the M. triangularis. Huber is very insistent on this.

Should such a condition arise that the muscle in this region be truly derived from the platysma this would not interfere with the above classification. Exceptions there are to any rule, and in this case, it would be explained by stating that the caput buccale was absent and its function and place taken by aberrant fibres from the portio modiolaris M. labialis platysmae.

An admixture of fibres, some from the caput buccale and some from the portio modiolaris platysmae, can be imagined as existing to form the so-called M. risorius. This has actually been described by Kudo.

(4) In the above-mentioned article by Bluntschli (p. 244), he described in detail the many and various forms of positions occupied by the M. risorius when it is derived from the M. triangularis. In its most complete form it is fan-shaped, stretching from the M. triangularis below, to the M. zygomaticus above. In its more usual form of a single muscle belly, the M. risorius may lie in any radius of this semi-circle. Though Bluntschli draws the conventional M. triangularis in all his diagrams, we may take it that in some at least, the caput longum would predominate. Then we should have a powerful caput longum supported posteriorly by a continuous fan of muscle comprising the conjoint capita latum and buccale.

This fan, comprising the caput buccale and caput latum, was actually found in the dissection of the foetal head and also in the head No. 2325.

Kudo(18) also figures a Japanese head with the fan very fully developed. It really comprises the capita latum and buccale of this article.

Moreover, from the dissection of H.B. 1, No. 2317 and the foetal head, it seems possible that a portion of this fan may even extend anterior to the caput longum.

Then the M. triangularis is naturally divided into two main portions:

(*a*) A powerful muscular belly arising at or near the tuberculum mentale and comprising the caput longum.

(*b*) An almost complete semi-circular sheet of muscular fibres arranged fanwise around the modiolus. These fibres are not nearly so powerful as the caput longum and are extremely variable in their distribution.

The fan is practically never complete and the most cephalic portion is usually separated by a very wide gap from the remainder of the semi-circular sheet and forms the caput buccale. With regard to the remainder of the semi-circular sheet or fan, this also differs widely in extent in different subjects, which is the cause of such discrepancy, as we have seen in various representations of the muscle from so eminent and careful observers. This forms the caput latum and, as we have already mentioned, it shares with the platysma and probably other facial muscles, the ability to act in sections.

Such are the considerations which have led to the abandoning of the term M. risorius and the re-naming of the muscle the "caput buccale M. triangularis."

It seems as though the caput latum and caput buccale form the radii of a circle whose centre is anterior to the modiolus and about the region of the mouth angle, though often one or other of these heads may not reach the circumference of such a circle. At present, there is not sufficient data to state whether there is any interrelationship between the size of these two heads; if, for instance, when the caput buccale was small we got the smaller type of caput latum and *vice versa*. But in the heads under dissection, this is certainly true, for in H. B. 1 and No. 2317, the caput buccale is very small and the fibres of the caput latum fall very far short of the margin of the mandible.

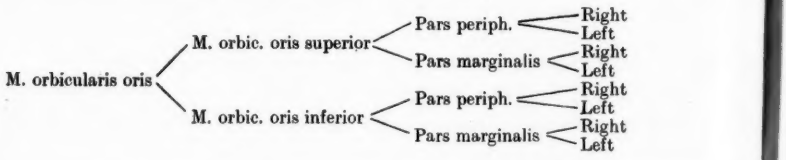
In No. 2325 there is a very well-marked caput buccale, and here the caput latum reaches as low as the margin of the jaw and forms the typical triangular muscles as figures in Spalteholz.

M. ORBICULARIS ORIS

(Table C, 20, 22, 25, 26, 33, 34)

In Eiler (*l.c.* p. 137) a summary is given of the different theories with regard to the M. orbicularis oris; originally considered as an orbicular muscle similar to the orbicularis oculi, it has more lately been thought to be composed of four or even eight different portions. This latter has been adopted in the present article and has been confirmed by the dissection of the various heads.

Diagrammatically stated, the position is as follows:



All the authorities are not agreed upon the separate entities of the pars peripheralis and pars marginalis, but in the following description it will be seen that there is no alternative to each being separately described and treated.

No true orbicular or circular fibres could be found, the nearest approach to this being found in H. B. 1, where a few fibres from the inferior pars margi-

nalis encircled the angle of the mouth and became continuous with the pars peripheralis superior.

Again, the modiolus is taken to be the area of insertion of all the muscles entering it except the M. orbicularis oris for which it forms an area of origin.

Arising from their respective modioli, the orbicularis oris fibres of the one side end by decussating in the median plane with their fellows from the opposite side. Only occasionally does there seem to be a direct continuity of fibres. Occasionally in the lower lip there may be a raphe(10).

Pars peripheralis or corpus of the muscle consists of the main bulk of the muscle extending from the rima oris outwards in an ever-thinning sheet. It reaches as far as the septum nasi above (pars nasalis or depressor septi), the sulcus mentolabialis below. (This is only approximately true, for in very well-developed muscles it may extend a little lower and, of course, laterally it takes origin from the modiolus.)

On section, it is seen that the muscle does not all lie in the one plane, but near the rimal and thickest portion of the section it is uniform or hook-like. It is the hook-like formation which joins it inseparably from the pars marginalis (Table C, 20, 22, 33 and 34). The section is therefore sickle-shaped, and macroscopically its fibres are directly continuous with and pass imperceptibly into the pars marginalis. This sickle or hook-like shape always is more pronounced in the lower than in the upper lip.

The pars peripheralis lies approximately in the centre of the lip and its muscle fibres are interlaced with and pierced by fibres from the labial tractors which pass through it to gain insertion into the fibrous tissue beneath the mucous membrane of the lip. This is to be seen only in microscopic sections.

Pars marginalis, as the name denotes, consists of the marginal fibres of the M. orbicularis oris. They do not lie in the same plane as the pars peripheralis fibres, but lie anterior to it, in the form of a crescent so that when viewed in sections the whole muscle presents the form of a hook. The tip or point of the hook almost reaches the skin at the point of junction of the skin and lip red.

The pars marginalis, unlike the pars peripheralis, does not extend for the whole length of the lip. It is limited to the red lip area and would therefore seem to vary in different subjects according as there is much or little red lip showing. As has been already stated the terminal portion or insertion of each pars marginalis is covered by the lip red and here lies directly anterior to the pars peripheralis. But, if we trace these fibres from their insertion back to their origin, we find that they turn round the rimal edge of the pars peripheralis, and proceed along the deep or posterior surface of the pars peripheralis to gain origin in the modiolus, immediately anterior to the mucous membrane of the vestibule and cheek, and posterior or deep to the origin of the pars peripheralis.

The formation of the pars marginalis indicates its mode of action. Taking origin in the deepest portion of the modiolus just adjacent to the mucous membrane, it curls around the whole thickness of the pars peripheralis and eventually lies wholly anterior to this. It follows from this, that contraction

of the pars marginalis must tend to bring downwards and slightly forwards, the medial portion of the pars marginalis, and therefore also the lip red (cf. Table C, 22 and 23).

Apart from this action, which we shall presently see, leads to the formation of labial cords (q.v.) the contraction of the M. orbicularis oris as a whole, can only be to close the rima oris in much the same way as if one were to have two pieces of elastic attached at each end to the modioli, and were then to pull the two modioli apart.

The antimeres to the M. orbicularis oris must therefore open the rima oris and the antimeres are the M. quadratus labii superioris above and the M. quadratus labii inferioris and portio labialis platysmae below, i.e. the labial tractors. Now the superficial (*b*) fibres of these labial tractors are in both lips inserted into the deep tissues of the red lip area, posterior and at right angles to the pars marginalis and probably are present in the philtrum of the upper lip.

The superficial (*a*) fibres, i.e. skin fibres of the labial tractors, vary slightly in the two lips. In the upper lip their fan-like spread does not extend laterally further than the red lip area nor into the philtrum. In the lower lip, owing to the great obliquity of the portio labialis platysmae, their lateral insertions only extend as far laterally as the red lip area, but they meet in the median plane.

This seems true both of the European and the Australian aboriginal. But in the upper lip of the Australian aboriginal, fibres from the caput laterale M. malaris extend into the upper lip and apparently act as an extra labial tractor of the outer third of the upper lip.

(N.B. No sections of this portion of the upper lip have as yet been examined but the macroscopic appearance seems clear.)

There is nothing to correspond to this in the European faces and so it would seem that in the European, independent movements of the outer third of the upper lip have been lost and this brings it into line with the lower lip. May not this account in some way for the feebleness of the so-called "canine sneer" in European races?

In *Homo sapiens* the pars marginalis is triangular in section with the apex of the triangle, abutting against the skin and its base, resting upon the sickle-shaped pars peripheralis.

It is partially separated from the corpus or pars peripheralis of the muscle by a constant stream of muscular fibres from the labial tractors which pass between the two divisions of the M. orbicularis oris to be inserted into the fibrous tissue beneath the red lip area.

Ruge states (*l.c.*) that when a muscle becomes interrupted by bone and its distal portion acts as a separate entity then this distal portion may show a great increase in size (Table F, 7). This statement was made by Ruge with regard to the M. quadratus labii inferioris and the platysma. No mention was made with regard to the innervation of the separated portion of the muscle, but it is evident from the consideration of these two muscles that the M. quad-

ratus labii inferioris has not the same innervation as the original muscle from which it is separated.

It may therefore be added as a corollary that the distal separated portion of a muscle need not retain the innervation of the parent muscle.

This is a particular statement and may be generalised. Then it would read that, if for any reason, the distal portion of a muscle became separated or partially separated from its corpus and acts as a separate entity, then this distal portion may show a great increase in the size and number of its muscle fibres. In other words, the separated distal portion of a muscle behaves in a manner similar to a plant "cutting."

This would seem to be the case with the pars marginalis. In sections of the lips of a female chimpanzee, this hook-like formation was also investigated as it differed very materially from those already described. The chimpanzee seemed to show a stage of transition between the fully formed M. orbicularis oris, consisting of a pars marginalis and pars peripheralis and the more primitive type, consisting of a pars peripheralis only (Table C, 25 and 26). In the upper lip there is practically no retroversion of the lip margin, and we see the primitive M. orbicularis oris. In the lower lip there is a very well-marked retroversion of the lip margin forming at first sight the typical hook-like formation as seen in *Homo sapiens*. But there is a very marked difference between the simple turning back of the margin of the lip and the formation of a pars marginalis. In the chimpanzee the whole muscle was in one piece and no division could be detected between a pars marginalis and a pars peripheralis. The hook-like shape was merely a retroversion or more probably a retroaction by the labial tractors of the margin of the M. orbicularis oris.

There was also noticed one other point of difference. In the upper lip of the chimpanzee the (*b*) fibres of the labial tractors penetrated between the terminal fibres of the M. orbicularis oris in much the same way as the corpus of the muscles.

In the lower lip this was also the case, but the (*b*) fibres of the labial tractors which penetrated between the fibres of the retracted portion were less powerfully developed than those penetrating the corpus.

This is a point of resemblance to the lip of *Homo sapiens* in whom few, if any, of the (*b*) fibres penetrated through the pars marginalis.

Duckworth (7) has investigated microscopically the shape of the M. orbicularis oris in man and many animals, though he does not state the position in the lip whence the sections were obtained, nor yet the amount of red lip visible, nor if it be absent; nor does he distinguish between the pars marginalis and the pars peripheralis M. orbicularis oris. He states that the gorilla, tarsius, paramelidae and lower forms of animal life show no trace of the hook-like formation of the M. orbicularis oris, but that this hook-like formation is present in a modified form in the chimpanzee and is well-marked in the Hereroes, Australian aboriginal and European races. This suggests that so long as the M. orbicularis oris was used as a prehensile organ and was extremely powerful

at its margin as well as in its corpus, the pull of its powerful antimeres would have but little effect upon its form.

But when the lips ceased to be prehensile organs and were being used in a modified way for speech then the marginal portion would become weaker and be dragged slightly forwards and upwards by the powerful M. quadratus labii superioris and forward and downwards by the equally powerful M. quadratus labii inferioris and portio labialis platysmae. Originally, this action would have exposed some of the mucous membrane of the mouth, which, in course of time would be modified and form our present red lip area. We find a similar example of the process in man's speech of to-day. In saying words like two, "oo," etc. or in pursing of the lips, we find the labial tractors acting very powerfully and the red of the lip pulled peripherally to such an extent that some of the mucous membrane may be exposed at the rima oris (Table C, 15 (*c*)).

The pars marginalis may therefore be regarded as a speech modification. There is another aspect of the action of the orbicularis oris which must not be forgotten as it recalls its more primitive function. It is true of this muscle as of many others, that a muscle primitively used for purely physical purposes may later be used for expressing similar intellectual processes.

Once used solely for the prehension of food, in higher races, it is in vigorous action when the individual seizes an opportunity or wrenches victory from an opponent (21).

From the preceding, it will have been gathered that the amount of the pars marginalis which lies directly anterior to the pars peripheralis M. orbicularis oris, is equivalent to the labial insertion of the labial tractors and both are defined on the skin surface by the amount of red lip showing when the lips are relaxed and closed. Therefore, with a powerful (and primitive) pars marginalis M. orbicularis oris and less or equally powerful labial tractors, we would expect little or no red lip showing. This has been shown to be phylogenetically the case and a similar condition may yet be seen in the faces of many men, giving to the face an expression of vigour and sometimes of cruelty. With a weak pars marginalis M. orbicularis oris and equally weak labial tractors, a similarly small amount of red lip might be expected.

It is a modified example of this latter which leads to the "short upper lip," which, though supposed to be a sign of beauty in women, is apt to give a doll-like appearance to the mouth.

With a weakened pars marginalis M. orbicularis oris but still powerful labial tractors, we might expect the maximum of red lip to be visible.

Such conditions are often seen and give to the face a sensual or voluptuous cast.

LABIAL CORDS

(Table C, 22, 23, 24)

In the production of sound there are two factors to be considered:

(1) The "stops."

(2) The amplifier and resonator. With the latter we have at present no concern. With regard to the former there are three sets of "stops":

(*a*) The vocal cords.

(*b*) The tongue. The "stop" is produced either by the back of the tongue impinging against the back of the hard palate as in "K," or the anterior portion of the tongue against the middle portion of the hard palate as in "J," or finally by the top of the tongue against the teeth or anterior portion of the hard palate as in "T."

(*c*) By the lips. The "stop" is here produced in two ways—either by the meeting of the two lips or by the pressure of the lower lip against the maxillary incisors.

That the lips have a very definite and musical function in the production of sound is stated by Wilmart (*La Clinique*, Bruxelles, 1897 (22), p. 364) who describes them as *anches membraneuses* (membranous organ-stops). Partly for reasons of anatomical nomenclature, but chiefly because it expresses more accurately their action, the lips when they assume this function will be alluded to in this article as "labial cords."

As in the vocal cords during vocalised sound, so it is in the labial cords in whistling and non-vocalised sounds. A stream of air under pressure is passed across an edge of muscle or elastic tissue covered by epithelium; a musical or contrary sound will ensue and the character thereof will depend upon the shape of the cavum oris, tongue, vocal and labial cords, as well as such individual characteristics as the shape of the nasal air cavities, etc. The consonantal sounds "P" and "B" for instance, are due to the bursting apart of the labial cords by the pressure of air behind them. The labial cords are formed in the consonantal portion of all the letters and words uttered by the subject but in none are they so well-defined and with such sharp edges as in the letters "P" and "B" (Table C, 3 and 6).

In the other sounds the labial cords are often much more rounded and cushion-like (Table C, 13 (*a*), 15 (*d*)).

As in the case of the vocal cords, the distance apart of the labial cords varies according to the sound emitted.

Also it will be noted that the lower lip may form a labial cord whilst the upper lip is merely slightly pursed or everted from the upper incisors as in saying the sound "V" (Table C, 4 (*c*)). In this case there is no activity of the superior pars marginalis M. orbicularis oris. In the formation of these cords quite new factors come into play. Here the pars marginalis is dominant and the terminal fibres of the M. quadratus labii superioris, M. quadratus labii inferioris and portio labialis platysmae, resistant.

If the action of the upper lip be described in detail it will be an easy matter to understand the similar working of the lower lip, always remembering that in the lower lip the M. quadratus labii inferioris and the portio labialis platysmae represent the M. quadratus labii superioris of the upper lip. In the upper lip then the labial cord is produced as follows (see Table C, 22, 23, 24).

We have seen that the pars marginalis not only is bowed upwards and anterior to the pars peripheralis in the median line, but laterally it is curled around the lower margin of the pars peripheralis to gain its attachment in the modiolus, posterior to the pars peripheralis. If, therefore, the pars peripheralis be fixed, as is always the case just previous to the formation of the labial cords, then, when the pars marginalis acts it must depress the lip margin and tend to thin it out. This thinning out of the lip margin is further accentuated by the terminal fibres (*b*) and (*c*) of the M. quadratus labii superioris which pass posterior to the pars marginalis and drag upwards the soft posterior portion of the lip. The result of this action of the terminal fibres (*b*) and (*c*) can often be seen in the living subject as a very marked linear depression at, or near, the region of junction of the mucous membrane and red lip.

That portion of the M. quadratus labii superioris which is inserted *en echelon* into the skin of the upper lip, i.e. the (*a*) fibres, acts as the resistant to the dominant pars marginalis.

Thus two firm ribbons or cords are formed by the red lip margin which at first resist and finally allow a quantity of air under high pressure to pass across them, thus giving rise to the consonantal portion of the sound.

In the above description of the labial cords no mention has been made of the much-discussed muscle of Klein because it seemed to be merely a part of the terminal fibres of the labial tractors. Looked at in certain sections, e.g. lower lip with oblique labial tractors, the muscle of Klein looked definite, but when the sections were fortunate in obtaining the muscle fibres cut in longitudinal section, e.g. upper lip just below the ala nasi, the supposed muscle of Klein was seen to be, in reality, a portion of the continuous stream of fibres proceeding from the labial tractors, which, in the upper lip was of course the M. quadratus labii superioris.

The action of this muscle of Klein would have been in some ways very similar to that of the labial tractors, though, of course, very local and confined to the lip margin.

Wilmart (22) describes the action of this muscle as follows: "Non dans la succion, mais dans le siffler et dans la prononciation des consonnes labiales, c'est-à-dire quand les lèvres fonctionnent comme anches membraneuses."

According to Ruge the muscle of Klein is absent in prosimians and lower primates; on the other hand, Bovero found it in these and in a large number of other mammals ((10), p. 130).

ANGLE OF THE MOUTH

From the description of the M. orbicularis oris one would expect to find that the angle of the mouth was more acute-angled and less rounded than is actually the case.

This rounded mouth angle is brought about by a very definite thickening of connective tissue of the deep fascia lying between the apex modioli and the mouth angle.

Fading away peripherally to a sheet much thinner than is usual, it presents at the mouth angle a very thick and definite crescentic border and after this it again becomes the thin and delicate perimysium of the rimal surface of the M. orbicularis oris.

This gives a smooth and even edge to the mouth angle and also makes a rounded mouth angle instead of a narrow slit-like fish mouth. Its thickened central border can be seen very distinctly in certain movements stretching from the mouth angle of the lowest point of the pars marginalis inferioris and in Table C, 2 (*d*) it has been called the angulo marginal ridge.

M. INCISIVI

Both the M. incisivi superioris and inferioris are very plainly seen in activity in the accompanying photos as they are one of the modiolar stays. Of all the facial muscles, none is so completely or so often visible in the normal person as the M. incisivus inferioris. In the faces of women, owing to the comparative insignificance of the facial hairs and their glands, the action of the facial muscles is much easier to observe and more often seen.

In some of these, the activity of the small M. incisivus inferioris is astounding. One can trace it almost from its origin to its insertion and may often observe slight asymmetry in the insertion, being more medial on the one side.

THE MODIOLUS

(Table C, 28, 29, 41, 42, 43, 44, 45)

In young healthy vigorous men with thin faces there is often seen just external to the angle of the mouth a definite rounded eminence with a well-marked vallum superiorly and laterally. This is best seen when the face is in repose and is due to the muscular modiolus lying immediately beneath, and over which in all faces the panniculus adiposus is especially thin (Table C, 29). The Germans have long recognised as an anatomical feature this thick mass of muscle lying just outside the angle of the mouth and have called it the Knoten (10). As far as can be gathered it is the thickness of this mass, and the fact that it is the meeting-place of so many of the muscles surrounding or running towards the rima oris on either side, and that their fibres became so intermingled in this mass that has attracted attention.

No definition is given of this mass nor any suggestion made that it is of more moment than being an anatomical area; just as the anterior fontanelle marks a definite bony gap so the Knoten marks a definite muscular mass.

But in this article it will be treated as an area of the greatest importance both anatomically and physiologically. Its strength and position enable the movements of the lips to be made with such precision and accuracy as are necessary for all forms of speech. To it will be applied the name Modiolus (L. *modiolus*—nave of a wheel) since the six chief muscles which enter into its composition form the radiating spokes of an imaginary wheel. (The caput longum and caput latum M. triangularis oris are here considered as two separate muscles.) The modiolus is the shape of a flattened cone with its base on the mucous membrane and its rounded apex beneath the thin and fibrous panniculus. The base is crescentic, the superior cornu being 0·6 cm. to 1·5 cm. medial to the angle of the mouth or the lateral extremity of the rima oris and 1·5 cm. to 2·6 cm. (vertically) superior to the rima oris. This cornu represents the most medial attachment to the mucous membrane of the M. zygomaticus. The inferior cornu is only 0·3 cm. to 0·5 cm. medial to the mouth angle, but it is very deep and slopes downwards and slightly laterally to attain a depth of 2·1 cm. to 2·5 cm. inferior to the rima oris.

This cornu represents the most medial attachment to the mucous membrane of the deep fibres of the pars peripheralis M. orbicularis oris and the deep fibres of the M. incisivus inferioris.

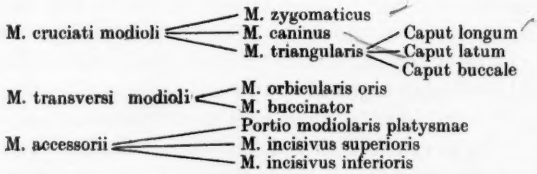
Obliquely across itslower third is a chain of large glands which lie amongst the fibres of the M. buccinator at their lateral extremity.

The total vertical depth of the modiolus just exterior to the angle of the mouth measures at the mucous membrane 3·6 cm. to 4·6 cm. The exact width of the base of the modiolus (i.e. measurement at the mucous membrane) is not possible to determine owing to the very close connection between the M. buccinator and the mucous membrane of the cheek. It is about 2 cm. wide, i.e. from the rima oris laterally and excluding the cornu.

The thickness of the modiolus is difficult to determine but was estimated as 1·0 cm. (H.B. 1).

The blunt apex is approximately 1 cm. lateral to the rima oris in all the heads dissected.

The muscles forming the modioli are:



The M. zygomaticus being antimeric to the caput longum M. triangularis and the M. caninus antimeric to the caput latum M. triangularis, there is thus formed a rough cross or X and it is this which has given to the group the name M. cruciati.

This anatomical antimerism will often be seen to be also true physiologically.

At first it was thought that this would always be true, viz. that if the M. caninus acted the caput latum would be in activity. Such is not necessarily the case, for the resultant of the activity of two or more muscles may be the antimere of a single muscle.

The modiolus represents the area of insertion of all the muscles which enter into its formation though as a general rule it serves rather as an area of origin than of insertion for the M. orbicularis oris. This muscle is peculiar inasmuch as in the pronouncing of a single sound it may at first use the modiolus as its insertion and to finish the sound use the modiolus as its area of origin, alternatively using its interlacement in the median plane as the area of origin or insertion.

As an example, the sound "OO" (Table C, 8 (*a*) and (*b*)) shows the M. orbicularis oris at first taking the median plane as its origin and dragging the modiolus forwards. When the modiolus has reached the point necessary for the true lip formation (consonantal portion) to take place, the musculi cruciati come vigorously and suddenly into action and fix the modiolus at this point.

From now onwards the M. orbicularis oris uses the fixed modiolus as its area of origin and proceeds to purse the lips to the extent necessary for the production of the sound. It is this fixation of the modiolus which enables it to be used as an area of origin by the M. orbicularis oris and gives to this highly specialised group of muscles their extraordinary range of movement and variety of function. From primitive prehension they take to themselves the difficulties and niceties of speech.

The position of the modiolus can be varied at will by the individual and it can instantly be fixed in any position.

With a base firmly fixed by muscular action the M. orbicularis oris is free to assume any position or perform any duty just as easily and efficiently as if it were attached to bone; and yet the fixed base can be varied many times in a minute.

The arrangement of the muscle fibres in this area is that of a series of fans spread out and interlacing with each other. Some of the fans are spread sagittally, others coronally, and there may be a mixture of both even in the same muscle insertion.

Hence we find the fibres of the same muscles lying immediately under the panniculus adiposus also in the centre of the aggerate muscle mass and again being inserted into the mucous membrane.

Most authors seem able to derive the M. orbicularis oris from one or other set of muscle fibres surrounding the rima oris. Santorini says from the M. buccinator—Albinus, from the M. caninus and M. triangularis and Gegenbauer and Ruge give in addition to the M. caninus and M. triangularis some semicircular muscles ((10), p. 317). Cunningham cleverly combines them all. Eisler states, however ((10), p. 115), "es ist tatsächlich nötig geduldig Bündel um Bündel mit der Nadel aus dem Knoten auszulosen, um dem oben geschilderten Ergebnis zu gelangen."

As he does not give us the result of such laborious work, we may presume he found it impossible. Such also was the case in the present dissections. The union of the fibres is so close and the interlacing so intricate, that it was not found possible to trace any commensurate body of fibres from one muscle into any other.

It is true, fibres and bundles of fibres from any one muscle may be traced into another muscle or muscles, but they did not represent a fraction of the bulk of either muscle, and all of course passed through the modiolar area.

By far the greatest number of fibres seemed to end in the modiolus, interlacing with similar fibres from an opposing muscle. No two fibres seemed to end exactly at the same level. As has been stated, very few of the fibres proceed into the belly of another muscle but the fibres that do so may be regarded as the anchor fibres, i.e. merely the extra necessary strengthening so that no muscle as it were, might pull itself out of the modiolus. These anchor fibres are to give strength to the modiolus and the muscle from which they spring, but do not in any other way enter into the composition of the muscle into which they proceed.

As the M. buccinator is a direct anatomical antimere to the M. orbicularis oris, it probably helps to control the modiolus, but only to a minor extent, and for the most part it, like the orbicularis oris, is free to perform its own functions between its lateral and median fixed points, namely, the lateral origin from bone and raphe and the medial modiolar insertion. It can do this easily, as its fibres when at rest are longer than the distance between the fixed points, and the cruciate modiolar muscles are relied upon for the fixation of the modiolus.

The depth from the surface, however, prevents us from making any examination unless these bellows are distended.

Its strong contraction therefore produces merely a flat surface between the two fixed points, and hence food is kept between the teeth. Its moderate contraction is quite sufficient to be an efficient help in controlling the modiolus.

Again, if this state of moderate contraction be maintained, and the air-pressure inside the mouth be increased, we shall have the M. buccinator distended and visible as in whistling.

This distension, which is not excessive, would represent the normal and true length of the muscle fibres, as they are when at rest, just as the tense ropes of a distended balloon cover represent the true length of the supporting structure which is so hard to estimate when the balloon is collapsed.

Here the mucous membrane represents the balloon and the M. buccinator the rope support. As this support is of muscle fibres, the tension on the modiolus during the act of whistling is constant, whether the M. buccinator be inflated or flat.

An attempt has been made to dissect three modioli with indifferent success. But the attempt was made with an open mind and without attempting to bolster up any preconceived notion as to the ultimate distribution of the muscle fibres which compose the modiolar agger.

Though a large number of the fibres could not be traced to any definite area but seemed to end in the aggerate modiolus still there were very definite insertions of muscles into the mucous membrane forming the base of the modiolus. This insertion into the mucous membrane has been fully described for many of the muscles by Eisler (10). Even these insertions do not seem to be constant either in size or position, but they are as a rule such large and easily identifiable muscle sheets that their presence is worth recording.

It is upon findings such as these, upon the general suggestiveness of the modiolar mass, and upon the confirmation obtained in the living subject as to its activities, that the preceding description of a modiolus was based:

Basis modioli. The following are the sizes of the different modiolar bases. The measurements were made by drawing a horizontal and a vertical line through the angle of the mouth and taking measurements from these lines.

H.B. 1. Apex modioli, 1·0 cm. lateral of angle of mouth.
Sup. cornu, greatest breadth, 0·6 cm. medial to vertical line.
Sup. cornu, greatest depth, 2·1 cm. superior to horizontal line.
Inf. cornu, greatest breadth, 0·3 cm. medial to vertical line.
Inf. cornu, greatest depth, 2·56 cm. inferior to horizontal line.

No. 2317. Apex modioli, 1·0 cm. lateral to angle of the mouth.
Sup. cornu, greatest breadth, 1·4 cm. medial to vertical line.
Sup. cornu, greatest depth, 1·65 cm. superior to horizontal line.
Inf. cornu, greatest breadth, 0·4 cm. medial to vertical line.
Inf. cornu, greatest depth, 2·5 cm. inferior to horizontal line.

No. 2325. Apex modioli, 1·0 cm. lateral to the angle of the mouth.
Sup. cornu, greatest breadth, 1·0–1·5 cm. medial to vertical line.
Sup. cornu, greatest depth, 1·65 cm. superior to horizontal line.
Inf. cornu, greatest breadth, 0·5 cm. medial to vertical line.
Inf. cornu, greatest depth, 2·0 cm. inferior to horizontal line.

The insertion of the different modiolar muscles will be taken seriatim, a general description given and then their insertions noted in each of the three subjects dissected (Table C, 28).

M. zygomaticus. The insertion of this muscle is divided into two separate portions, a superficial and a deep. The M. caninus passes between the two heads (10). This was easily recognised in all the subjects dissected. The superficial portion is derived chiefly from the lateral superficial fibres of the muscle. The deep portion is derived from the medial superficial and deep fibres.

Some fibres of the superficial portion form the most superficial layer at the apex modioli. Some cross the apex modioli to end in the modiolus itself, others pass beyond the modiolus and either enter the pars peripheralis M. orbicularis oris inferioris or else join the muscle fibres of the M. triangularis along its anterior border. In doing this they cross obliquely the M. triangularis just below the apex modioli. They are intimately bound to the fibres of the M. caninus and the M. triangularis which lie immediately beneath them. Other fibres pass along the lateral border of the modiolus to join with fibres of the

various capita of the M. triangularis, usually the caput buccale or even with the portio modiolaris platysmae.

The deep portion is inserted in two regions of the modiolar base:

(1) A large body of fibres proceed transversely medially to occupy the superior half and the tip of the superior cornu of the basis modioli. Here they lie at a deeper plane to the fibres of the M. incisivus superioris and pars peripheralis M. orbicularis oris, but superior to the insertions of these muscles into the basis modioli.

(2) The main body of the deep fibres which lie lateral to those just mentioned proceed obliquely downwards and medially more or less in direct line with the muscle belly of the M. zygomaticus. These fibres are inserted over an area extending downwards as far as the centre of the modiolus. Its fibres interlace with those of the M. buccinator and with the deep fibres of the M. triangularis.

Unlike the superficial portion of the M. zygomaticus which is very intimately bound to the canino-triangularis complex, the deep portion is separated from this complex by a loculated or "cellular" mass of delicate connective tissue which suggests a primitive multilocular bursa, whose function would be to absorb pressure. In consequence of this, the canino-triangularis complex is easily separated from the deep portions of those muscles attached to the basis modioli and the opposing surfaces of these two groups of muscles are smooth and shiny. It is transversely through this space that the external maxillary artery passes quite close to the angle of the mouth. This is contrary to the text-book teachings, though Spalteholz's diagram 836, vol. II, represents very accurately the course of the artery. This diagram shows quite clearly that the artery passes through the centre of the modiolus and the only place where this could take place is deep and not superficial to the M. caninus.

H.B. 1. *Superficial portion* very similar to the general description given above. In this subject, however, the superficial medial as well as the superficial lateral fibres formed the superficial portion of the muscle. The medial superficial fibres passed to the outer margin of the upper lip and covered the pars peripheralis M. orbicularis oris in a manner similar to the labial tractors.

The fibres crossing to the medial border of the M. triangularis were few in number.

Deep portion. Similar to general description. The deep portion of this muscle seemed to be chiefly composed of the deep fibres of the M. zygomaticus. There were two obstacles to the more exact description of this muscle: firstly, the large size of the pars peripheralis M. orbicularis oculi and the fact that it was in closer union with the M. zygomaticus than in the European, and secondly, that a large part of the dissection had been completed before it was realised that the pars peripheralis M. orbicularis oculi should be treated apart from the underlying muscles.

No. 2317. *Superficial portion* similar to general description, but no fibres were seen to enter the pars peripheralis M. orbicularis oris inferioris. As the

caput buccale is rudimentary, the fibres of the lateral edge of the M. zygomaticus join the caput longum fibres.

Deep portion. Similar to general description.

As the superior cornu of the modiolus was a large one the fan of the fibres was more extensive and spread out. The more medial fibres ran almost horizontally beneath the M. caninus, M. incisivus superioris and pars peripheralis orbicularis oris for a distance of 1 cm. medial to the angle of the mouth. The more lateral fibres formed the main bulk of the muscle and were inserted directly posterior to the M. caninus and slightly superior to the level of the apex modioli (i.e. to a horizontal line drawn through the angle of the mouth). In addition to these, others of these deep sets of fibres ran vertically downwards to join the deep surface of the M. triangularis.

No. 2325. The insertion of the muscle differs somewhat from the general description given above. There are still a superficial and a deep portion.

Superficial. This is formed by the whole of the superficial fibres of the M. zygomaticus. The lateral superficial fibres are inserted into the modiolus, much as has been described, by crossing the M. triangularis and curling around its anterior margin. The fibres of the lateral edge join the caput buccale M. triangularis on the right side and the caput latum on the left side. The median superficial fibres pursue a somewhat unusual course on both sides of the face. They do not pass deeply to the basis modioli but remain superficial and pass more or less transversely and medially to end in the lower portion of the nasobuccal gyrus and some seem to join the lateral edge of the M. quadratus labii superioris fibres as they lie anterior to the pars peripheralis M. orbicularis oris to form an accessory elevator of the upper lip.

Deep portion. On account of the aberrant distribution of the medial superficial fibres the M. zygomaticus has no representation in the superior cornu of the basis modioli. There is, however, a large body of fibres composed of the deep fibres of the M. zygomaticus, which proceed obliquely across, towards the modiolar centre and are attached to the basis modioli in this area, much as has been described above.

M. incisivus superioris. At its origin this muscle lies superior and posterior to the M. orbicularis oris, but it soon comes to lie in approximately the same plane. It is inserted into the modiolus in two portions—a superficial and a deep. The superficial portion comprises chiefly the median fibres of the muscle. As they approach the modiolus, these intermingle with the fibres of the M. caninus and finally end with them in the middle and upper portions of the modiolus. The deep portion consists of the more lateral fibres. They remain during the whole of their course somewhat more deeply situated than the median fibres and finally are inserted into the base of the modiolus (basis modioli) in the superior cornu, immediately superior to the angle of the mouth. They reach this by passing between the M. caninus and the deep portion of the M. zygomaticus, and are inserted immediately inferior to the zygomatic fibres.

M. incisivus superioris (H.B. 1). The insertion of this muscle was much as in the general description. The insertion into the basis modioli, though inferior to the deep head of the M. zygomaticus, did not reach the tip of the superior cornu of the basis modioli.

No. 2317. *Superficial portion.* These fibres joined the anterior fibres of the M. caninus and with them ended in the modiolar maze.

Deep portion. Though, for the most part these were inserted inferior to the deep portion of the M. zygomaticus some of them reached and occupied the tip of the superior cornu of the basis modioli. Here there was some interlacing with the fibres of these two muscles. Some of the deep fibres had also another insertion, viz. into the modiolar corpus. Others, having passed into the modiolus close to the basis modioli joined the deeper fibres of the M. triangularis.

No. 2325. Superficial portion enters the modiolus similarly to the general description.

Deep portion. Owing to the absence of a portion of the usual deep insertion of the M. zygomaticus in this subject, the deep portion of the M. incisivus superioris occupies the upper portion of the tip of the superior cornu, i.e. they occupy the position usually taken by the M. zygomaticus in the superior cornu. Moreover, they were at first taken for fibres of the M. zygomaticus as they run much more transversely and laterally than in the other modioli dissected.

M. incisivus inferioris. This muscle is likewise inserted in two portions—a superficial and a deep. The superficial portion comprises the superior fibres of the muscle which run upwards intermingled slightly with the lower border of the pars peripheralis M. orbicularis oris inferioris. They gain insertion into the modiolar mass in a manner similar to this muscle. It is these fibres which are so often seen in women in a stage of vigorous activity.

The *deep portion* is inserted into the inferior cornu of the basis modioli in its most medial and inferior parts. Some of the lowest fibres may pass and join either the M. buccinator or platysma, and others, to gain insertion into the periosteum of the mandible.

H.B. 1. *Superficial portion,* as described above.

Deep portion. (*a*) *Superior fibres,* as described above, but these fibres are divided by a group of larger mucous glands lying obliquely across the inferior cornu of the basis modioli. Some fibres pass superior but the majority inferior to these glands.

(*b*) *Middle group.* Other fibres join with both the M. buccinator and portio labialis platysmae. These run transversely outwards under the M. triangularis.

(*c*) *Inferior group.* In addition, there were fibres resembling the M. anomalus maxillae, which passed from a bony origin to a bony insertion, both points being immobile. These fibres ran horizontally and laterally for about 2 cm. and have been termed by Bardeleben the M. praemandibularis transversus (10).

No. 2317. The insertion of both portions was the same as the general description.

No. 2325. *Superficial portion.* Insertion very similar to the general de-

scription, but in addition a few of the superior fibres joined with a few of the inferior fibres of the pars peripheralis M. orbicularis oris, and these were inserted directly into the skin close to the apex modioli.

Deep portion. Superior fibres end in inferior cornu as described.

Middle fibres pass out more or less transversely beneath the M. triangularis. Some end by joining the portio labialis platysmae and others intermingle with or join the M. buccinator.

Inferior fibres. These passed transversely beneath the caput longum M. triangularis and the M. quadratus labii inferioris close to its origin. It was inserted into the periosteum in this region (M. praemandibularis transversus).

M. caninus. In a dissection of the facial muscles, if the skin and panniculus adiposus be reflected from the centre of the modiolus in a radiate fashion, one gets a very clear demonstration of the relationship between the M. caninus, M. incisivus superioris and pars peripheralis M. orbicularis oris. At first sight, they appear to form an unbroken radiating fan of muscle stretching from beneath the M. zygomaticus to the red lip margin. On further inspection the M. caninus fibres are seen to be somewhat coarser than those of the M. incisivus superioris and as one dissects further away from the apex modioli and approaches the origins of the muscle, the different components of this sheet become slightly separated.

The M. caninus is variable in its insertion and difficult to dissect as the majority of its fibres end by interweaving with the fibres of other muscles. It enters the modiolus between the deep and superficial portions of the M. zygomaticus. To the superficial portion of this muscle it is inseparably bound, but between it and the deep portion of this muscle, is a natural line of cleavage filled by loculated ("cellular") fine connective tissue. After this, its fibres spread out in all directions, resembling a rosette rather than a fan.

A large body of fibres are intimately bound to the under surface of the M. triangularis, so that it is impossible to say which fibres belong to the M. caninus and which to the M. triangularis. These fibres are from the medial portion of the muscle.

The lateral superficial fibres of the muscle apparently cross the apex modioli immediately beneath the superficial portion of the M. zygomaticus. The ultimate distribution of these fibres depends largely upon the type of M. triangularis present. If there is a well-developed caput latum they may join the fibres of this head as well as the caput longum M. triangularis, but if the caput longum is rudimentary, they enter or join the caput longum M. triangularis. In both cases it seems impossible to decide which fibres belong to the M. caninus and which to the M. triangularis. The deeper fibres of the M. caninus pass deeply through the modiolar network to gain insertion into the basis modioli inferior to the angle of the mouth. These may be a considerable body of fibres or there may be no attachment to the basis modioli. Other fibres again pass forwards into the pars peripheralis M. orbicularis oris inferioris or backwards into the M. buccinator. Many of the fibres of the M. caninus cannot be

traced to any definite insertion but end blindly in the modiolus, some superficially and others deeply.

H.B. 1. The insertion is much as described above and all portions are represented. Here, however, the fibres passing to the lateral edge of the M. triangularis were very few, whereas there was a very large body of fibres gaining attachment to the basis modioli.

No. 2317. The insertion was much as in the general description, but no fibres entered either the M. orbicularis oris superioris or inferioris and no body of fibres gained attachment to the basis modioli, but a large proportion of the fibres of this muscle seemed to end blindly in the modiolus at all levels.

Owing to the rudimentary nature of the capita buccale and latum, the lateral fibres of the muscle after crossing the apex modioli beneath the superficial fibres of the M. zygomaticus appeared to curl around the lateral border of the caput longum M. triangularis.

But as the lateral fibres of the caput longum were also twisted upon themselves, it was impossible to say which fibres belonged to the M. caninus and which to the caput longum M. triangularis. A few of the medial fibres of the M. caninus proceeded medially deep to the superficial portion of the M. incisivus superioris. Other fibres again joined the deep surface of the caput longum M. triangularis.

No. 2325. The insertion of this muscle is much like the general description given above. Many of the superficial fibres enter both the caput latum and caput longum M. triangularis. Also, there was a very well-marked bundle of fibres which were inserted into the basis modioli. These came from the deeper fibres of the muscle and the whole of this insertion lay inferior to the angle of the mouth.

M. triangularis. The insertion of this muscle will be described according to its component capita. The capita latum and buccale for this purpose may be considered as one muscle. With them it is convenient to describe the insertion of the portio modiolaris platysmae. These sheets of fibres enter the superficial area of the modiolus and cannot be traced to any definite location. Occasionally, fibres from some other of the modiolar muscles may be traced into any or all three of these sheets, or these fibres might be considered as being derived from these sheets and entering the other modiolar muscle. Beyond that, one can only say that all three are inserted into the modiolus by interlacement with the other muscle fibres which compose it.

Caput longum. Just as the whole of the M. triangularis is an extremely variable muscle both in size and composition, so also does the caput longum vary greatly in its size and mode of origin, and consequently in its mode of insertion. No. 2317 presented a well-developed caput longum which took origin not only from the tuberculum mentale but also lateral and medial to this. It will be taken as a type, and its insertion described in detail (Table C, 42). The muscle naturally divided into three portions, medial, central and lateral. The medial fibres, comprising many of the fibres arising from the

tuberculum mentale and all those arising medial to it, passed deep to the main body of the muscle by curling around the median border of the upper third or half of the muscle, much in the fashion of the insertion of the M. pectoralis major. These fibres passed obliquely upwards as a muscle band, lying just posterior to the centre of the modiolus to gain insertion into the basis modioli immediately inferior to the most posterior fibres of the deep portion of the M. zygomaticus (Table C, 28). Some few of these fibres also join the upper fibres of the M. buccinator. The curling of fibres around the median margin of the M. triangularis helps to round its margin.

A large body of lateral fibres form into a thicker, though less, broad sheet of muscle and this curls around the lateral and upper third or half of the central portion of the muscle and come to lie directly anterior to it at the apex modioli. These fibres end by interweaving with the lateral superficial fibres of the M. caninus as already described. The central portion of the muscles proceeds upwards towards the modiolus narrowing though thickening as it does so. Just below the apex modioli it is criss-crossed superficially by two bands of muscle. The one band formed from its own lateral fibres crosses it obliquely from below upwards and medially, and the other formed from the superficial head of the M. zygomaticus which crosses it and the previous band obliquely in a downwards and medial direction. These bands not only strengthen, thicken and round the upper parts of the lateral and median borders of the M. triangularis but also cause the upper central portion to appear depressed. These central fibres end chiefly by interweaving with the M. caninus. A definite bundle of them, however, pass directly into the pars peripheralis M. orbicularis oris superioris.

Another definite bundle of them end in the modiolar mass by interlocking at an angle with the pars peripheralis M. orbicularis oris inferioris.

From the above, it will be seen that the triangular shape of the muscle is not only due to the muscle fibres merely gradually altering their respective planes of incidence, but also by definite portions of the muscle curling themselves around the remainder. Also it will have been noted that here again, we have a deep as well as a superficial attachment of the muscle to the modiolus, and, in addition, a large body of the fibres entering the centre of the muscle agger.

Were it not for the presence of a well-marked caput buccale in Miss X's face, it might have been thought that her M. triangularis was of this character.

H.B. 1. Here again the capita latum and buccale were small and their insertions were as stated above. The caput longum did not show the elaborate arrangements of No. 2317 nor the large lateral attachment to the basis mandibulae. It was inserted into the modiolus very similarly to No. 2317. The deep attachment to the basis modioli was similar but was derived from the posterior or deep central fibres of the muscle.

No. 2325. The three heads of the M. triangularis are well-developed in this subject. The fibres of the caput buccale and a few of the caput latum cross

superficial to the caput longum and then fade away in the modiolus. On the right side the caput buccale crosses the modiolar area just below the apex modioli and a few fibres blend with the fibres of the superficial portion of the M. zygomaticus at the anterior border of the caput longum.

On the left side the fibres of the caput buccale and a few of the caput latum cross the caput longum well below the modiolar area.

Caput longum. Some of the deeper lateral fibres interdigitate with the inferior fibres of the pars peripheralis M. orbicularis oris inferioris below the inferior fornix and therefore below the modiolus. They may possibly be inserted into the inferior cornu of the basis modioli.

No fibres could be seen to pass to the M. buccinator and there was no rounding of the median border due to such fibres. The main body of fibres took origin from the tuberculum mentale and ran obliquely upwards to enter the modiolus. Here it was difficult to trace the fibres, but some joined the M. caninus and some the M. incisivus superioris.

M. transversus menti (caput transversum) was a well-developed muscle sling lying under the chin. Its fibres lay in part superficial to the lateral fibres of the caput longum, but in part they seemed to lie completely lateral to this head and to be directly continuous with, and form part of, the caput latum. The fibres extended from modiolus to modiolus and had no bony attachment.

Beneath the chin they lay superficial to the most medial fibres of the portio mandibularis platysmae.

Caput latum is a broad well-developed muscle fan directly continuous with and on the same plane as the M. transversus menti just mentioned. Its fibres are of varying length being longest medially and shortest laterally. The fibres of this head enter the superficial surface of the modiolus lateral to the caput longum and are covered by the fibres of the caput buccale and superficial portion of the M. zygomaticus. The total width of the combined capita latum and longum is at the basis mandibula 3·55 cm. and just below the apex modioli 1·68 cm.

Caput buccale. This head is well developed. It takes origin in the cheek 1·3 cm. superior and 4·5 cm. lateral to the angle of the mouth. It is a thin muscle band 0·8 cm. wide, which enters the superficial portion of the modiolus and forming with the superficial portion of the M. zygomaticus the most superficial fibres of the modiolus. Some of its superior fibres curl upwards to be continuous with the most lateral fibres of the M. zygomaticus.

Foetus (8/12*ths*). The deep dissection of this head has not yet been attempted and it is doubtful if it will be possible to do so with any degree of accuracy. The superficial dissection, however, was productive of many points of interest as will be seen in the orthoscopic tracing (Table C, 45).

The M. triangularis had three well-developed heads though the capita latum and buccale formed a single continuous and large fan of muscle stretching from the lower pole of the corpus adiposum buccale laterally downwards and medially to completely cover the caput longum M. triangularis and for

some distance, medial to this head. The fibres medial to the caput longum were not so long as the other fibres of this fan, but they were well marked and completely covered the M. quadratus labii inferioris and the portio labialis platysmae fibres which lay medial to the caput longum.

The whole fan was of remarkable thickness and stood in bold relief to the subjacent platysma. The caput buccale consisted of the superior fibres of this sheet which ran almost transversely across the cheek from the lower pole of the corpus adiposum buccae to gain the superficial portion of the modiolus. Caput latum fibres formed the remainder of this muscle fan. Its fibres lateral to the caput longum were of a more uniform length than in the adult and the more median of these fibres extended well below the basis mandibulae. It apparently completely covered the caput longum.

Caput transversum. This muscle was well marked and seemed to be very definitely derived from the caput latum and to really form part of it. As elsewhere described, it formed a complete sling, stretching from modiolus to modiolus. In this specimen one could not help making comparisons between the M. transversus menti and the caput buccale. Both seemed integral parts of the caput latum but the latter, due to its usual dissociation from the main mass and the former owing to its unusual and striking distribution, have been given names other than that of the parent corpus. If then, the one may be called the caput buccale ought not the other to be called the caput transversum?

That the caput transversum should be considered a special part of the caput latum and possess a different name is shown by No. 2317. Here there is a well-marked caput transversum though the capita latum and buccale are vestigial. There are several peculiarities of the capita transversum and latum that require special attention. Firstly, they both lie wholly superficial to the platysma and generally their fibres run more or less transversely to the fibres of the platysma. They are, therefore, the most superficial muscle fibres in this region.

Secondly, they tend to form a collar around the cephalic portion of the neck, i.e. the submental and sublingual regions. Some fibres, i.e. the caput transversum, actually do so and the fibres lateral to this endeavour to do so, but the two sides are separated by ever increasing intervals as we proceed away from the caput transversum. This seems to fulfil the conditions of a sphincter colli superficialis. Hence, it is suggested that the capita transversum, latum and possibly also the caput buccale, represent in man that variable muscle sheet seen in the lower mammals, the sphincter colli superficialis.

Caput longum. This muscle was completely covered by the two preceding muscles. It took origin from the region of the tuberculum mentale but no fibres lateral or medial to this took origin from bone.

M. buccinator. Though, there is interlacement of fibres between the different portions of this muscle, nevertheless there remains enough individuality of the separate portions to justify the description of the insertion

according to the mode of origin of the fibres, i.e. the uppermost fibres from the maxilla and hamulus, the middle fibres from the pterygo-mandibular raphe and the lowermost fibres from the mandible. The uppermost fibres run obliquely downwards, the middle fibres more or less transversely and the lowermost fibres twist outwards then medially to form a fan-like sheet approaching the modiolus. The deep fibres from all three heads are so closely bound to the mucous membrane of the cheek that it is impossible to separate them satisfactorily from it. It is, in fact, an area of insertion for some of the fibres of this powerful muscle. The modiolar insertions are as follows:

The uppermost fibres are inserted into the basis modioli immediately lateral to the insertion of the deep heads of the M. zygomaticus and triangularis. All the upper fibres seemed to end in this manner, and no bundle of fibres passed to any other muscle, though a few strands may have done so.

The middle fibres are very closely united to all the modiolar muscles and are difficult to trace. A very definite, though intriguing sheet of fibres passed to the under surface of the M. cruciali modioli. They apparently did not run directly into these muscles but curled forwards to reach and then backwards along their under surfaces. The remainder of these fibres end either in the modiolus amongst the muscle network, or by interlacing the fibres of the pars peripheralis M. orbicularis oris. Some of these fibres apparently enter this muscle in both the upper and lower lips. Some fibres probably also enter the pars marginalis M. orbicularis oris, but this part of the dissection is extremely difficult to be exact in, because of the intimate connection of both muscles with the basis modioli.

The lowermost fibres must be considered in two groups, a superior and an inferior. The superior end, like the middle fibres just described, in the modiolar base just below the angle of the mouth by interlacing with the fibres of the M. orbicularis oris inferioris fibres. Few strands seemed to be directly continued into this latter muscle as the two muscles met each other at a slight angle. A large proportion of the inferior fibres pass under the M. triangularis and then forwards to reach and end in the fibro fatty areolar tissue of this area. Some may even reach the skin. A few of the deepest of these fibres are inserted into the most inferior portion of the inferior cornu of the basis modioli in the same area as the deep group of fibres from the M. incisivus inferioris. There seemed to be an exchange or interweaving of fibres between the two muscles. There was also an interchange or interweaving of fibres between this portion of the muscle and the pars peripheralis M. orbicularis oris inferioris, but none reached the pars peripheralis M. orbicularis oris superioris.

H.B. 1. Much as described above.

No. 2317. Much as described above. Apparently in this subject no fibres of the M. buccinator entered the upper lip and few the lower lip.

No. 2325. Much as described above. But in this subject there was a very marked interchange of fibres between the M. buccinator and the deep portion of the M. incisivus inferioris.

M. orbicularis oris. The two portions which comprise this muscle, viz. the pars marginalis and the pars peripheralis, will be described separately. The pars marginalis has a deep and superficial origin from the modiolus, but the pars peripheralis has a superficial middle and deep origin. In fact, if the modiolus were cut into slices or sections parallel to the basis modioli, each section would be found to contain its quota of fibres from the pars peripheralis M. orbicularis oris. Both lips will be described as the M. orbicularis oris behaves differently in the upper and lower lips.

Though the M. orbicularis oris chiefly uses the modiolus as its area of origin, it also uses it as an area of insertion. In describing the muscle it will be regarded as an area of insertion and so keep it comparable to the other muscles of this area.

In both lips, the pars marginalis is closely bound to the "red lip" wherever the two are in contact and a dissection can only be made by shaving off the "red lip." Until the pars marginalis curls around the rimal edge of the pars peripheralis, it is in close contact all the time with the "red lip" and were it not for the fact that the "red lip" extends further into the vestibule than the pars marginalis, it might have been said that the two were co-terminous. In both lips also the pars peripheralis is inserted into portions of the cornua and into the basis modioli. But medial to this, the pars peripheralis has no attachment either to the "red lip" or to the mucous membrane of the vestibule. A wedge of fibrous tissue with its apex anteriorly is interposed between the muscle and the mucous membrane and "red lip" which enables them to be dissected apart with the greatest ease.

Upper lip, pars marginalis, superficial portion. These fibres are few and do not sweep round the rimal border of the pars peripheralis and they may be absent. When present, their insertion is variable; sometimes they may be quite superficial and near the apex modioli; at other times, they may lie deeper and join the pars peripheralis M. orbicularis oris inferioris.

Deep portion. The main body of fibres sweep around the rimal border of the pars peripheralis and are inserted into the body of the basis modioli. Here they spread out fan-wise and interlace with similar fibres from the pars marginalis inferioris. They lie inferior to the deep head of the M. zygomaticus, M. incisivus superioris and M. triangularis and are separated from them by deep fibres of the pars peripheralis M. orbicularis oris superioris.

Pars peripheralis. In surface view this muscle is very broad in the median line and appears to become very much narrower laterally. At the mouth angle, however, this muscle has become very much thicker, and as far as can be judged, contains its original number of fibres. This twisting of the muscle upon itself enables the muscle to spread its fan in an antero-posterior direction and so embrace all planes of the modiolus.

The superior fibres become anterior and the inferior fibres posterior.

Superficial portion. These fibres enter the apex modioli just below the panniculus adiposus. Some enter the superficial surface of the M. triangularis

and some enter the pars marginalis inferioris. A large number end in the modiolus in this region.

Deep portion. These are inserted into the superior cornu and body of the basis modioli. Here they lie between the deep fibres of the pars marginalis superioris inferiorly, and the M. triangularis, zygomaticus and incisivus superioris, superiorly.

Central portion. In between these two groups lies a large body of fibres passing into the centre of the modiolus where a large number of them end. Some, however, enter the M. buccinator and a few enter the pars marginalis inferior.

Lower lip, pars marginalis. Like the pars marginalis superior, this muscle has a superficial and a deep insertion.

Superficial. These fibres may enter the superficial surface of the modiolus close to the apex modioli, or they may pass deeper and curling around the angle of the mouth, enter the pars peripheralis superioris. When they enter the modiolus they are amongst the most superficial of the fibres of the lower lip, but they lie deep to those superficial fibres from the upper lip, notably those from the pars peripheralis superioris, which join the superficial surface of the M. triangularis. To this is partly due the appearance that the upper lip overlaps the lower at the angle of the mouth.

Deep portion. These fibres curl around the rimal margin of the pars peripheralis inferioris to gain insertion into the inferior cornu and body of the basis modioli where they spread out fan-wise and intermingle with the fibres of the pars marginalis superioris.

Pars peripheralis. Superficial fibres pass into the modiolus deep but intimately bound to the M. triangularis. Some of these fibres also join the pars marginalis superioris.

Deep portion. These fibres curl upwards to be inserted into the inferior cornu and body of the basis modioli. Here they lie between the M. incisivus and caninus below, and the pars marginalis inferioris above. They meet at an angle to and interdigitate freely with the inferior deep fibres of the M. buccinator and some fibres enter this muscle.

Central portion. In between these two portions lie a very large body of fibres which pass into the centre of the modiolus chiefly to end here. Some apparently enter the M. buccinator.

H.B. 1. *Pars marginalis superioris.* There was no superficial portion; otherwise much as general description.

Pars peripheralis superioris. Much as general description.

Pars marginalis inferioris. Of the superficial fibres, some enter the centre fibres of the pars peripheralis superioris—others of them enter the modiolus, as in the general description.

Pars peripheralis inferioris. Much as general description.

No. 2317. *Pars marginalis superioris.* Superficial fibres end in the pars peripheralis inferioris. These lie deep to similar fibres from the pars marginalis inferioris which enter the pars peripheralis superioris.

Deep fibres end in basis modioli, similarly to general description.

Pars peripheralis superioris. These are inserted much as in the general description. However, only a few fibres joined the M. triangularis.

Pars marginalis inferioris. The superficial fibres join the pars peripheralis superioris and they lie superficial to the similar fibres from the pars marginalis superioris.

The deep portion is inserted similarly to the general description.

Pars peripheralis inferioris. These are inserted much as in the general description.

No. 2325. *Pars marginalis superioris.* Superficial portion consisted of a weak band of fibres which entered the superficial area of the modiolus near the apex.

Deep portion. This curled around the rimal edge of the pars peripheralis and was inserted much as in the general description.

Pars peripheralis superioris. This followed the usual plan insertion.

Pars marginalis inferioris. Superficial portion. This was a particularly well-developed band of muscle which curled around the angle of the mouth to enter the pars peripheralis superioris. To gain this, it passed between the two portions of the pars marginalis superioris.

Pars peripheralis inferioris. The insertion was very similar to the above description. The only unusual feature was the insertion of some of the lowest fibres into the skin just external and a little below the angle of the mouth. These fibres were accompanied by a few of the superior fibres of the M. incisivus superioris.

Conclusions. From the preceding it will be seen that allowing for great variations in size and general intermingling of the various fibres, there still remain some constant factors on which to base the conception of a modiolus.

These are the constancy of deep and superficial insertions of the various muscles, and in many cases, the constancy of their relations to each other.

Then the basis modioli has certain areas fairly definite and constant as areas of insertion of the deep portions of many of the muscles. Finally, no sufficient body of fibres could be found passing directly from one muscle into another to give the impression that the one muscle was in reality a derivative of the other. The only exceptions to this might be the M. caninus and M. triangularis.

Further physiological confirmation is forthcoming later in this article.

M. MENTALIS

(Table C, 14 (*b*), (*d*), and 20)

Judging by the descriptions of careful and well-known observers the M. mentalis is subject to much variation and this seems to have obscured the real action of the muscle. As observed in the Australian aboriginal, the muscle consists of two main portions—a median and a lateral. The fibres from each

of these portions arise similarly from the fossula incisiva and run in parallel directions, being spread out in the shape of a vertical fan. The upper fibres of this fan run horizontally forwards, or even may be inclined slightly upwards, whereas the lowest fibres run almost vertically downwards. The lateral fibres are inserted directly into the skin of the chin, whereas the median fibres interlace with their fellows of the opposite side to form a series of arches or loops.

In both the Australian aboriginal and the European No. 2325, some of the most lateral fibres took origin from the incisiva fossa as usual, but proceeding vertically downwards were inserted into the tuberculum mentale in a way exactly parallel to the anomalus maxillae. These fibres can have no effect upon the action of the main muscle, and will not be taken into account in the following description. Similar fibres have been described by Eisler(10) under the name anomalus menti.

As to whether these loops of muscle fibres ultimately reach the skin there is at present no information and the dissection of the Australian aboriginal was complicated by the whole of the chin being covered superficially by fibres of the M. quadratus labii inferioris. It seems probable that some of them do reach the skin on the opposite side of the chin.

This condition of a series of loops has been described in Europeans both by Virchow(31) and Eisler(10). The centre of these loops is not an empty space but is completely filled by a large pad of very firm fibrous tissue below and at times a smaller pad of fat above this and in direct contact with it.

Behind the fibrous tissue pad and separating it from the mandible is a small bursa. This allows the pad of fibrous tissue to slide more easily over the underlying bone.

This is the condition we should expect to find in those people whose chins are smooth and rounded.

But in people with a dimpled or cleft chin, we might expect to find the M. mentalis as described by Spalteholz and Cunningham. Here there are a few or no median loops but most or all the fibres on each side are inserted into the skin of the chin on the same side. In these cases, the dimple or cleft of the chin is due to the skin being bound to and drawn inwards by the fibrous tissue pad lying between the two muscles. Thus, in the one case, we have a complete muscular cylinder surrounding a fibrous tissue pad, and in the other, an incomplete muscle cylinder, inasmuch as its anterior wall is formed by the skin which is also adherent to the underlying fibrous tissue pad. Nevertheless, the action of the muscle will be the same in both cases, though more easily understood if we study the more primitive type as seen in the Australian aboriginal and many Europeans.

Taking the muscle of both sides to form a single working machine, we find that the whole apparatus forms a very efficient double action pump. It differs from those ordinarily in use only in the fact that the walls of the cylinder are movable and thus act not only as a guide or barrel for the piston, but also as the force which propels the piston.

The muscular loops, of course, form this movable cylinder wall, the firm connective tissue pad is the piston and the mobile, but highly incompressible, fluid is represented by the fatty pad (Table C, 20). Again, the top end or head of the cylinder is formed and closed completely and firmly by the interlacement of the M. orbicularis oris and the M. quadratus labii inferioris. The lowest fibres of the M. orbicularis oris also often interlace with the upper fibres of the M. mentalis. When, therefore, the muscular cylinder tries to expel its semi-fluid contents, it exerts great pressure against the cylinder head and moves the cylinder head cranially. But as the cylinder head consists of the muscles comprising the lower lip it must mean a cranial movement of the lower lip.

We thus see that the activity of the M. mentalis pushes the lower lip either directly upwards, or upwards and forwards, and the actual position taken is dependent upon two causes:

(*a*) The position of the upper lip and the degree of contraction of the M. orbicularis oris superioris.

If the upper lip is held out of the way by the fingers or by the M. quadratus labii superioris, or if the M. orbicularis oris superioris be very flaccid then the activity of the M. mentalis will push the lower lip directly upwards.

If the M. orbicularis oris superioris be firmly resistant, then the activity of the M. mentalis will lead to a very firm pressing of the lips together.

(*b*) The relative resistance of the M. orbicularis oris inferioris and M. quadratus labii inferioris.

If the M. orbicularis oris inferioris is weakly resistant and the M. quadratus labii inferioris strongly resistant, then the activity of the M. mentalis will result in the lower lip being pushed forwards as well as upwards.

In this case the lip edge will roughly describe the arc of a circle whose centre will be the point of origin of the M. quadratus labii inferioris.

The semi-fluid fatty pad ensures an equal distribution of force over the whole cylinder head. This ram-like action enables the lower lip to be pouted or protruded in spite of the modiolus being fixed in a posterior or neutral position; an accomplishment that otherwise would be impossible. It is a movement quite peculiar to the lower lip and not possessed by the upper lip. The action of the M. mentalis therefore is quite unlike that of any other skeletal muscle and its nearest counterpart in the human body is the contraction of the heart. The muscular activity described above, is greatly facilitated by the skin of the chin being raised at the same time. This is brought about mainly by the lateral portion of the M. mentalis which is inserted directly into the skin.

In this way it not only raises the skin of the chin but also forms a second though incomplete muscle cylinder, which assists in raising the piston of fibrous tissue.

In doing this, it creates small pits or depressions in the skin of the chin which have long been recognised as signalising the activity of the M. mentalis.

In the commencement of this article we described the M. mentalis as being

a double action pump and until now we have been considering only the upstroke where the M. mentalis is dominant and the M. orbicularis oris and M. quadratus labii inferioris, resistant. Now we must consider the downstroke where the M. quadratus labii inferioris and M. orbicularis oris are dominant and the M. mentalis is resistant.

This is very well exemplified in the pronouncing of certain consonants, e.g. "P" and "B," in laughter, etc. Here the cylinder action is reversed. The cylinder head presses down the fatty pad and hence the pad of fibrous tissue, and this in turn pushes downwards the whole cylinder wall or M. mentalis.

At the same time the M. quadratus labii inferioris flattens or compresses the whole cylinder and its contents against the mandible so that the engine now resembles a flattened ovoid rather than a rounded cylinder.

Finally, we may compare the M. mentalis and the pars transversa M. nasi.

Both have somewhat similar areas of origin.

Both are in the form of muscular loops.

Both enclose or partially enclose a mass of fibrous or semi-fibrous and cartilaginous tissue.

Both are utilised in speech.

Both are indirectly associated with the modiolus by their respective M. incisivi and is shown in diagram 17, Table C.

FACIAL CREASINGS AND THE PANNICULUS ADIPOSUS

There seems to be an impression that one of the functions of the facial muscles is to crease the skin and that all the facial muscles are sending a constant succession of small fibres to be inserted into the corium.

With the exception of the upper and lower lips, the eyebrows and perhaps part of the eyelids, that has not been found to be the case. The function of the facial muscles is to open, close or distort the shape of the facial apertures and any facial creasings that may result are exactly comparable to those in a curtain drawn back by the hand to enlarge the aperture of light.

It is true some muscles send fibres or groups of fibres to end prematurely in the panniculus adiposus, but this is not the rule. Were it so, we should expect, on the analogy of the M. quadratus labii superioris, to get a very serious diminution in the size of the muscle before it reached its insertion.

More rarely, we find offshoots of muscle fibres entering the corium of the skin and blended so closely with it, that it is impossible to dissect off the skin without at the same time cutting across the strands of muscle. These must be the cause of dimples. A very good example of this was seen in No. 2325, in whom on the right side the superficial fibres of the M. incisivus inferioris entered the corium over the modiolar area.

Occasionally, a tendon was seen in connection with the facial muscle, e.g. in D.B. 2, the caput buccale arose from the fat of the cheek just below the zygomatic arch by a very well-marked tendon. This was an interesting curiosity.

No profusion of tendons was found such as are described by Eisler(10) as being the usual mode of ending of many of the facial muscles.

In the causation of facial creasings, the rôle played by differing thicknesses of the panniculus adiposus is second only to the pull of the facial muscles. A brief description of this panniculus will therefore be given.

In the accompanying diagram (Table C, 40) the various thicknesses of the panniculus adiposus is indicated by vertical lines and the closer the lines, the denser the fat. When there was a large amount of dense fibrous connective tissue, whether or no it were accompanied by fat, it has been indicated by a series of dots. The bare areas in the diagram indicate that there was little or no superficial fibrous or fatty tissue intervening between the skin and subjacent muscles. In the diagram there are two such bare areas:

1. Involving the greater portion of the upper lip including the lip red and also the lip red of the lower lip.

2. Small areas near the margins of the upper and lower eyelids. It will be noticed that in the upper eyelid this area is greater than in the lower lid.

There are five areas where the subcutaneous fibrous tissue is very dense:

(1) An ovoid surrounding both eyes though not corresponding with the M. orbicularis oculi area. The major portion of these areas contains also fatty tissue but in the lower eyelid there is a crescentic area with little or no macroscopic fat.

(2) The tip and alae of the nose are formed chiefly of the dense fibrous connective tissue.

(3) The philtrum.

(4) The whole of the chin and lower lip. Here there is an intermingling, in regions very considerable, of fat with the fibrous tissue.

With regard to the varying density of the panniculus adiposus it is most dense in the naso-buccal gyrus and thinnest in the forehead, upper and lower eyelids, bridge of the nose and lower lip. The naso-buccal gyrus is seen most typically in the Australian aboriginal and the European infant (Table C, 30). In the Australian aboriginal the portion covering the bridge of the nose is very marked in the adult, but in the aboriginal infant, it is of course much more evident. This is present in the European infant, but in the adult is very rudimentary or absent, and this is one of the reasons for the seeming absence of any bridge to an infant's nose. In the adult, the portion about the naso-labial furrow becomes greatly enlarged in corpulent people and there must be a great wasting of the panniculus adiposus to cause the fat to entirely disappear from this region.

The remainder of the face is covered by a more or less evenly distributed layer of fatty tissue and of special note is the spectacled arrangement around the eyes and across the bridge of the nose. If, for the time being, we exclude from consideration the more or less immobile nose, the area between the sulcus naso-labialis above, and the sulcus mento-labialis below is occupied by the highly mobile muscular lips and their modioli. Themselves covered by little

or no fat, they are almost surrounded by the fatty envelope of the face and this enveloping curtain ends somewhat abruptly at the above mentioned sulci.

As the lips act as solid bodies, their being drawn laterally and upwards (e.g. in laughing) throws the enveloping fatty curtain into folds, much as any curtain would do. These folds or creases naturally are at right angles to the direction of the muscular traction.

This is on the whole true of most of the facial creasings, that they are due to the folding or creasing of the fatty curtain and that these foldings are at right angles to the muscular traction. Camper ((8), p. 296) stated "that the contraction of each muscle of the face produced in the skin one or more folds, of which the direction is always at right angles to that of the muscle."

These folds in the skin may be produced in two ways:

1. The simple falling into folds like a curtain as cited above.

2. A thicker or more solid portion of the panniculus adiposus being drawn up against a thinner area of the panniculus. Here the thicker area acts like a cushion throwing into folds the thinner area of the panniculus, and therefore the skin. This is most typically exemplified by the action of the caput angulare M. quadratus labii superioris throwing into folds the skin over the root of the nose. A very interesting and unexpected example of this also occurs in the outer portion of the lower lip.

The most lateral 2–3 creases in the lower lip nearest the angle of the mouth are outside the area acted upon by the portio labialis platysmae. Though all the creasings of the lower lip are approximately parallel and run obliquely downwards and outwards, the most lateral ones are due to the action of the M. incisivus inferioris drawing the massive modiolus with its firmly adherent though thin panniculus adiposus, downwards and inwards towards the looser and equally thin panniculus adiposus of the lower lip. In this case, the dense modiolus takes the place of the denser layer of panniculus adiposus like the naso-buccal gyrus already mentioned. This downwards and medial movement of the modiolus is probably effected by the M. incisivus inferioris and it is this action of the M. incisivus inferioris which often gives to the angle of the mouth a look of great severity.

But there are two regions which do not seem to comply with the rule of Camper and where the skin creasings seem to be parallel instead of at right angles to the direction of muscular traction, viz. portions of the oral lips and the ocular lids. In the lower lip the creasings more medial to those mentioned above are parallel to the fibres of the portio labialis platysmae. That they are also caused by these fibres is easily to be seen by observing the face of elderly people, especially women, with "lined" faces.

In the upper lip also there are creasings which are parallel to the fibres of the M. quadratus labii superioris. These of necessity do not extend laterally or even as far as the most lateral extent of the red lip seen when the lips are closed and the face in repose. But like the similar creasings in the lower lip they can be seen in the process of formation in the lips of most elderly female faces.

As has already been noted, the more rudimentary condition of the hairs and their appendages makes the female face much more suitable for the observation of muscular action.

In the lower eyelids we see the peculiar admixture of both kinds of creasings, the central portions being parallel to, and the peripheral portions which are continuous with the central, being at right angles to the muscle fibres of the M. orbicularis oculi and M. malaris (caput laterale). In the upper eyelids the horizontal creasings are due rather to the M. levator palpebrae superioris than to the M. orbicularis oculi.

With regard to the facial creasings, Cowper's precept may be re-stated thus: "That where muscular action alters the relative position though not necessarily the shape of the panniculus adiposus, the resulting creasings will be at right angles to the line of muscular action, e.g. the cheeks and forehead. But, where the muscular action alters the shape though not the position of the panniculus adiposus, then if the panniculus adiposus be thin, there will be creasings of the skin parallel to the muscular fibres, e.g. eyelids and lips."

PHYSIOLOGY

In the study of the muscular activities necessary for the production of certain words, it must be borne in mind that in a cinematograph reproduction and especially in a slow-moving picture, each word will necessarily be split into its fundamental elements. Appended in Table E is a classification of the vowel and consonantal sounds, which has been supplied me by the Superintendent of the Deaf, Dumb and Blind Institution (H. Earlam, Esq.). This has been adhered to in the following descriptions:

It will be noticed that each of the letters B, F, M, OO, P, V is a combination of a vowel and consonant, sometimes the one, and sometimes the other, being at the beginning. The only exception to this is the sound "OO" and even here a doubt may be expressed as to its being a pure vowel sound.

Throughout, a marked feature in the utterance of sound was the very great difference in muscular activity required for a non-vocalised and a vocalised sound, e.g. "P" and "B." The non-vocalised sound required much more activity than the vocalised.

The same difference was also noticed between the consonantal and vowel sounds, the former requiring much greater muscular activity. When, therefore, the sound "OO" was seen to require such great muscular exertion, it was concluded to be composed of a consonantal sound akin to whistling and a vocalised vowel sound. These, of course, occur simultaneously, but it is the consonantal sound which gives the distinctive position to the lips and buccae. And it is this elongation into a tube-like structure of the cavum oris which changes the pure vowel sound into the resonant and somewhat booming "OO." Again, if we take into consideration the shape of the lips, they are definitely formed into labial cords which contribute in no small measure to the altered quality of the sound (compare Table C, 8 (*b*) with 7 (*a*)). As far as can be

gathered from this series of pictures, the formation of labial cords is only to be found in the consonantal sounds and this seems another strong argument in favour of considering the sound "OO" to be a mixed consonantal vowel sound. In addition to this, we notice that the pars transversa M. nasalis is in activity. Hitherto this has only been noticed in consonantal sounds.

Lastly, if the explanation offered here with regard to whistling be accepted, it seems impossible to deny to the sound "OO" its non-vocalised consonantal portion.

Another point that is very clearly illustrated is the constant and sometimes very great activity of the pars transversa M. nasalis in the production of sound. The degree of contraction of this muscle seems to depend upon two factors:

(*a*) the degree of activity of the M. orbicularis oris with which it varies directly. The greater the contraction of this muscle, the greater will be the contraction of the pars transversa M. nasalis. Under this head, of course, come such variations as are caused by axiom (Table F, 8);

(*b*) the kind of sound produced, whether it be a "closed" sound, e.g. "P" and "B" or an "open" sound, e.g. "F" and "V."

The words "open" and "closed" have here been used in a special sense to indicate whether the cavum oris is closed or open anteriorly during the production of the sound or until the actual production of the sound forces its anterior wall open.

The customary terminology did not explain all the different kinds of sound (viz. breath, vocal and nasal) in their relationship to the activity of the pars transversa M. nasalis in addition to the vocal and labial cords.

In the closed sound, the labial cords are kept tightly closed and allow the air pressure to increase behind them until it can finally burst them apart with an explosive sound. It is to help to completely close the cavum oris that the pars transversa M. nasalis occludes or attempts to occlude the posterior vestibular nasal space and hence to close the nasal cavity and prevent the loss of pressure. In this connection, it must be noted that the consonantal sounds "P" and "B" are the only ones in which the cavum oris is maintained as a closed cavity until the lips are burst apart by the air pressure behind them, and it is in these sounds that the pars transversa M. nasalis is in the strongest contraction.

In the consonantal sound "M" though the cavum oris is and remains closed anteriorly, it is open posteriorly and the air escapes through the posterior nasal space.

With regard to the term bursting the lips apart in the production of the sounds "P" and "B" some small explanation may be due. This is literally true for the amount of pressure being exerted at the time by the pars marginalis M. orbicularis oris, but it does not mean that the cavum oris is not able to maintain a much greater pressure. This, however, would entail a much more vigorous contraction of the pars marginalis M. orbicularis oris than would be consistent with the activities of speech.

In the open sounds "F" and "V" there is a constant stream of air issuing through the oral "stops" and though this is under pressure, there is not the same need to prevent the escape of air through other channels; and indeed, this would be unlikely with the large opening in front of the cavum oris, through which the air is already streaming to produce the sound.

With regard to the activities of the pars transversa M. nasalis, there is another point of view brought out by the consideration of these open and closed sounds, "B," "P" and "V," viz. that the pars transversa M. nasalis is only active if the M. orbicularis oris is dominant and that the more dominant the latter, so will the former be more active.

In "B," "P" and "M" the cavum oris remains closed anteriorly—in "B" and "P" until the lips are forced apart by outside pressure and in "M" until the sound is completed. In the two former, the pars transversa M. nasalis reaches its greatest activity, and in the sounds depicted "M" comes next in the vigour of this muscle's action. Of the open sounds, "F" and "V," the activity of the pars transversa is only feeble, but in these also the upper lip is only feebly pursed and takes a very minor part in the formation of the sound. Similar reasonings apply to the nasal vocal sounds. But in these cases we have further to consider whether there is any formation of a nasal chord by the pars transversa M. nasalis. Like the labial cords, it is a muscle covered by epithelium over which a stream of air is passed, but it is difficult to think it can have any sound producing properties.

On the other hand, one would expect that if the sound was produced solely by the vocal cords and palate, the pars transversa would be relaxed and the pars alaris active, so as to expedite the escape of air. The very fact of the pars transversa being definitely active in these cases suggests the function of a primitive cord.

NEUTRAL POSITION[1]

(Table C, 2 (*b*))

This is the first active position assumed by the mouth and lips when a person begins to speak and it is constantly recurring between different words. It is also the last active position to be assumed before the face returns to rest.

A slight indrawing of the breath necessitates the opening of the mouth; this is done by bowing the centre of the lower lip, the upper lip meanwhile remaining stationary. The movement of the lower lip is due to the dominant inferior labial tractors and the resistant pars peripheralis M. orbicularis oris. The swelling which occupies the lateral and superior margin of the sulcus mento-labialis is the pars peripheralis M. orbicularis oris, which is outlined by the contracted inferior labial tractors as though by a tightly fitting garment. The modiolus is fixed by the M. zygomaticus and caput longum M. triangularis.

In the median line there is an indication of the free margin of the M. quad-

[1] The term "neutral" is taken from the language of the motor, being that position of the gear lever from which any gear is available and to which it must return in changing to another gear.

ratus labii inferioris as is shown by the gap in the continuity of the swelling caused by the pars peripheralis M. orbicularis oris.

The Movement of the Facial Muscles in uttering the sound "B" (Table C, 3)

Consonantal sound (*vocal explosive labial*) "*B*." Having attained the neutral position the separation of the lips becomes more pronounced by the opening of the jaw, and separation of the teeth.

This probably starts synchronously with the opening of the lips though it appears to be later in time (i.e. after the lips have opened). The earliest opening may, in all probability, be due to the portio mandibularis platysmae acting synchronously with the portio labialis platysmae. The upper lip is stationary during this movement. As to whether these two portions of the platysmae can act separately, there is no information (in this patient the action of the portio labialis platysmae does not cause pitting and flattening of the red lip either in this movement or in laughing). The mouth being slightly opened and the teeth just separated as stated above, the modiolus is fixed early, and after that the M. orbicularis oris comes into action, the upper and lower portions acting slightly differently.

The fixing of the modiolus more strongly than before is brought about by the action of the following muscles, viz. M. zygomaticus portio modiolaris platysmae, the whole of the M. triangularis (capita buccale, latum and longum).

As these muscles come into play they draw the modiolus slightly backwards and it is here, i.e. a little posterior to the neutral position, that the modiolus is ultimately fixed.

It will be noticed that the M. zygomaticus here consists of two parallel muscle bellies, each inserting into the modiolus. By this posterior fixation of the modiolus when the lips act, they are closely pressed against the teeth all the time, and there is no pursing of either lip.

In pressing the lips together the pars peripheralis M. orbicularis oris is strongly dominant and the labial tractors strongly resistant. It is difficult to say whether the M. buccinator is in activity but one would expect it to be resistant to the M. orbicularis oris. But when the lips are as tightly pressed together as this the pressure of the lower lip is strengthened by the activity of the M. mentalis, which even may cause the lower lip to project slightly beyond the upper. This does not necessarily take place.

But with the M. mentalis dominant, the pars peripheralis M. orbicularis oris and the M. quadratus labii inferioris are resistant to it. We, therefore, have the unusual condition of the same muscles being at the same moment both dominant and resistant, viz. the pars peripheralis M. orbicularis oris inferior being dominant to the inferior labial tractors, and resistant to the M. mentalis. Also notice that the portio labialis platysmae, when resistant, does not show the marked swelling that will be noticed when it becomes dominant.

This is due to two causes:

(*a*) Its muscle fibres, though tense, are stretched and not contracted.

(*b*) The M. triangularis is acting strongly enough to overcome the muscle swelling present beneath it at that moment.

Notice close to the orbit the marked swelling and in the upper lip the linear ridges due to the activity of the M. quadratus labii superioris. With the lips now firmly closed by the dominant pars peripheralis M. orbicularis oris and its resistant muscles acting very vigorously, we now notice the red lip acting very strongly, and being pursed up into two firm ribbon-like cushions, whose edges are firmly and accurately approximated and resisting the rising air pressure behind them, i.e. the formation of "labial cords."

In the formation of the labial cords the pars marginalis M. orbicularis oris is dominant and the labial tractors resistant, i.e. fibres (*a*) of the labial tractors. Towards the end of this portion of the sound, the pars peripheralis M. orbicularis oris becomes less dominant as the labial tractors and especially the inferior labial tractors become increasingly active until they quite obliterate the upper portion of the caput longum M. triangularis. This weakens to some extent the closure of the lips and enables the air pressure finally to burst apart the labial cords. With the escape of air through the labial cords, all the muscles previously in activity quickly relax, though some more completely than others. In addition to the above labial movement, it is interesting to note the powerful action of the pars transversa M. nasalis, whose activity becomes increasingly active as the contraction of the M. orbicularis oris becomes stronger. Finally, it is suddenly released when the M. orbicularis oris ceases to be dominant. The sudden springing open of the external nares at this moment is very striking. The activity must primarily occlude (almost completely) the post-vestibular portion of the nose, but in so doing it also compresses the alae nasi and narrows the external nares.

As we might expect (Table F, 8) this activity is best seen in the consonantal sound "P" being the non-vocalised counterpart of "B."

Vowel sound (*lingual palatal*—"*EE*"). With the modiolus fixed by the M. zygomaticus and the three heads of the M. triangularis which are still strongly in contraction, the lips slowly open. As the lower lip bows itself downwards, we find the swelling of the portio labialis platysmae remains. Ultimately, the lower teeth are fully exposed, almost or actually showing the gums. This means that the portio labialis platysmae is now dominant and the M. orbicularis oris resistant. At this stage also we again see well marked the ridge just below the red of the lower lip. This ridge is best marked when the lip is fully drawn. During this time, the M. quadratus labii superioris has been dominant also, acting upon the central portion of the upper lip, bowing it up to expose the teeth slightly.

This dominant pull of the labial tractors as the lips approach the position requisite for the formation of the vowel sounds and in consequence the fibres of the portio labialis platysmae become less and less evident. When the

desired position is reached there is established an equilibrium and we see no longer the fibres of the portio labialis platysmae as definite ridges. Instead, we see only a rounded swelling indicating the area where the still dominant inferior labial tractors cross and cover the M. orbicularis oris. During this period the modiolus has gradually returned to the neutral position and the modiolar muscles become much less in evidence and their activity lessens *pari passu* with the activity of the M. orbicularis oris and its antimeres. Finally, when the full vowel position has been reached, only the M. zygomaticus and the caput longum M. triangularis oris are visible. This is quite sufficient to fix the modiolus as the vowel sound requires much less vigorous muscular activity than the consonantal. The condition remains till the end of the vowel sound. When that is finished, the dominant pull of the muscles antimeric to the M. orbicularis oris lessens and the lips return to the neutral position.

The Movement of the Facial Muscles in uttering the sound "P"
(Table C, 6)

Consonantal sound (*breath explosive labial*) "*P.*" This is very similar to "B"; the modiolus at first is fixed by the M. zygomaticus, caput longum, M. triangularis and portio modiolaris platysmae. A little later, the caput buccale acts though not very strongly at first and after that the caput latum and the incisivus superioris comes into play. There is slightly greater activity of the superficial modiolar muscles in forming "P" than "B."

Otherwise the movements are practically indistinguishable from those of "B." This holds true also of the vowel sound which follows. The vigorous contraction of the pars transversa M. nasalis is very well seen and perhaps easier to follow than in the sound "B."

The Movement of the Facial Muscles in uttering the sound "M"
(Table C, 5)

(1) *Vowel sound* (*lingual palatal "e" as in bet*) "*M.*" Starting with the neutral position where the M. zygomaticus is well defined as the movement progresses (Table C, 5 (*a*)) we see the M. zygomaticus getting less and less active until it reaches the resting position. After this it again comes into great activity. The mouth and lips are opened much wider, the M. caninus and caput longum M. triangularis and portio modiolaris platysmae fixing the modiolus. The labial tractors are dominant and the M. orbicularis oris resistant. The under lip is depressed sufficiently to allow the lower gum to be just visible. At the same time the upper lip is slightly retracted due to the M. quadratus labii superioris being dominant, and the M. orbicularis oris resistant. The edges of the upper incisors are just visible and the upper part of the naso-labial fold is obliterated.

(2) *Nasal vocal consonantal sound* ("*M*"). We now notice in Table C, 5 (*b*) though the mouth and lips are still fully widely open, that the swelling caused

by the portio labialis platysmae lessens the M. orbicularis oris remains well-defined and more fibres of the caput longum M. triangularis become visible. At the same time the portio modiolaris platysmae remains active. This must indicate, although there is absolutely no lip movement visible for some time, that the M. orbicularis oris is definitely dominant and the labial tractors resistant. At the same time the M. quadratus labii superioris becomes less active and the M. zygomaticus comes now practically to the position of rest (i.e. minimal activity). Then the lips begin to close, but it is a very purposeful and active process, and calls forth great muscular activity. The modiolus is drawn slightly backward and firmly fixed by the M. zygomaticus and M. triangularis (three heads), M. incisivus superioris and portio modiolaris platysmae. The lips meanwhile are closing and the M. mentalis is in a state of activity. During the closing of the lips the M. orbicularis oris is dominant. The portio peripheralis is dominant to the labial tractors and forms the firm basis for the portio marginalis, which here forms again labial cords but not so vigorously as in the sounds "P" and "B," as the sound is a nasal rather than a labial one. That the pars marginalis is in very strong contraction is evidenced by the angulo-marginal ridge being so distinctly seen. The activity of the pars transversa M. nasalis is visible though not marked, but the M. quadratus labii superioris is actively resistant and again obliterates the upper portion of the naso-labial fold.

(3) *Period of relaxation*, "*M*." We now notice that there is a slight pursing of the lips and the M. quadratus labii superioris becomes more active and the portio labialis platysmae obliterates the upper portion of the caput longum M. triangularis. During the whole of this process, however, the lips are in firm contact.

Next, the lips open again.

The modiolus is still fixed by the M. zygomaticus portio modiolaris platysmae and the three heads of the M. triangularis, but the caput buccale is not visible for long, owing to the puffing out of the M. buccinator. As the lips open, the superior and inferior tractors become dominant and the M. orbicularis oris resistant, though the labial cords are still maintained. This period is a very short one and not essential to the production of the sound.

In the formation of the sound "M," when not forming part of a word, it is probably always present as it allows to escape most easily the residuum of compressed air through the opened lips instead of through the nose.

The Movement of the Facial Muscles in uttering the sound "OO" (Table C, 8)

Vowel sound (*labial*) "*OO*." Owing to the letter "M" ending with pursed lips the earlier movements in this sound were omitted by the patient. The consonantal and vowel portions are here combined into one sound and do not occur separately.

This causes some confusion of muscular action as though the modiolus were uncertain whether to support the dominant M. orbicularis oris in the consonant sound, or the equally dominant M. quadratus labii superioris and inferioris and portio labialis platysmae in the vowel sound.

It is very hard to say whether the M. orbicularis oris or the labial tractors are dominant.

There is also indirect evidence of this confusion of muscular activities. As has been noted, the pars transversa M. nasalis acts during speech only when the M. orbicularis oris is dominant. Its activity in this sound would therefore seem to indicate that the M. orbicularis oris is dominant.

On the other hand, the failure of the lips to close and the excessive activity of the labial tractors would, under any other circumstances, have led us to conclude that the labial tractors were dominant. Both groups are acting so strongly and powerfully, the one to approximate and the other to bow the lips, that a new position is created and the lips are pursed. The new position is rendered possible by the initial lack of fixation of the modiolus by the cruciate modiolar muscles, thus allowing the modiolus to be dragged very far forward.

Then, and then only, is there any adequate sign of muscular activity in the modiolar muscles, and they become strongly active. The muscles that are in activity are the M. zygomaticus, capita longum and latum M. triangularis and the M. buccinator.

With regard to the M. zygomaticus and the caput longum of M. triangularis, it is to be noticed that owing to the anterior position of the modiolus, they are now acting at an angle to each other, and no longer approximate to the condition of a straight line. Their combined action would therefore be distinctly antimeric to the orbicularis oris.

But the very strong action of the M. orbicularis oris necessitates some stronger fixation of the modiolus, and this is brought about by the action of the M. buccinator, some of whose fibres are actually visible in the angle between the caput latum M. triangularis and the M. zygomaticus.

The M. buccinator here is not inflated by air pressure from within, but acts as an antimere to the M. orbicularis oris.

Notice also how the parotid duct is dragged forwards. Notice also in the lip that the fibres from the caput angulare are medial, i.e. towards the philtrum, and from the capita infraorbitale and M. zygomaticum are lateral and extend as far as the red lip normally visible (see Table C, 2 (*a*)).

It is worthy of note here, that the action of pursing the lips, apart from the creation of any sound, is brought about in an exactly similar way to this, though the action of the muscles is more powerful (see Table C, 14 (*c*)).

The portio marginalis again forms the lips into rounded cushion-like labial cords.

The pars transversa M. nasalis is very active here and again we notice that the strength of its action corresponds to the activity of the M. orbicularis oris.

THE MOVEMENTS OF THE FACIAL MUSCLES IN UTTERING THE SOUND "F"
(Table C, 4)

(1) *Vowel sound (lingual palatal short "e" as in bet)* "*F.*" We start here at the end of the neutral position. Next the jaw opens but far more widely than is the case with the letter "B," and as the mouth opens, we notice the tongue being curved forwards with its tip directed downwards, and apparently free. During the period of opening of the mouth cavity and even before the aperture becomes wider than is the case in saying "B," one notices a marked difference in the action of the M. zygomaticus.

In saying "B," as the mouth opened, it became more and more pronounced, but now it becomes progressively slacker until it comes almost to the position seen when the face is at rest, though the caput longum M. triangularis is still acting strongly. But partially obliterating and just anterior to the inferior or labial end of the naso-labial fold a new swelling is seen, caused by the action of the M. caninus. The M. caninus above and the caput longum M. triangularis below, meeting at an obtuse angle, tend to draw the modiolus towards the medial plane.

The action of the caput longum M. triangularis is only partially antagonised by the M. caninus, owing to the angle at which they set to each other being less than 180°. But with our idea of a perfectly balanced action of the facial muscles, this necessitates a third muscle to act upon the modiolus, in this case to balance the resultant of the two forces represented by the M. caninus and the caput longum M. triangularis.

The third muscle in this sound is the portio modiolaris platysmae as these fibres are distinctly visible near the margin of the mandible.

If the caput latum M. triangularis is also acting, it must be very feebly, as the fibres are quite obscured by the strongly acting portio labialis platysmae; the lower margin of the M. orbicularis oris is also well defined by the dominant M. quadratus labii inferioris and portio labialis platysmae as we saw in the vowel sound of "B." The M. orbicularis oris is, of course, resistant. During this period it will be also noticed that the M. quadratus labii superioris is dominant and the upper M. orbicularis oris muscles resistant, thus exposing slightly the upper teeth.

The action of the M. quadratus labii superioris in this sound gives us a very accurate idea of its lateral insertion into the lip.

Notice also the action of the tongue and the ridge below the M. zygomaticus caused by the parotid duct in its passage across the cheek.

(2) *Consonantal sound.* (*Breath continuous labial dental.*) The mandible now closes slightly and the modiolus returns to the neutral position, where the muscular activity is very small.

As this is taking place the M. orbicularis oris becomes dominant, and the labial tractors resistant, hence the swelling disappears from below the modiolus

and the whole of the M. triangularis is seen in action, and the fibres of the portio modiolaris platysmae are seen more clearly than heretofore.

Once the neutral position has been gained, the M. orbicularis oris (portio peripheralis) becomes actively dominant both in the upper and lower lips. Each had a different action.

This dominant activity at first drags the modiolus slightly forwards but it is fixed almost immediately by the strongly acting M. caninus, M. zygomaticus, M. triangularis (three heads) and the portio modiolaris platysmae, and later also the M. incisivus inferioris. This fixation allows the M. orbicularis oris to act with freedom and certainty and the M. buccinator to be but slightly resistant, and so to act as a delicate and efficient bellows. The upper lip is protruded slightly and held rigidly away from the teeth and slightly above their lower edge. Whether the pars peripheralis M. orbicularis oris is dominant and the M. quadratus labii superioris resistant, or *vice versa*, it is hard to say.

The position of the lips is brought about by two factors:

(1) The most important is the early fixation of the modiolus in a slightly anterior position.

(2) The powerfully opposed and synchronous action of the M. orbicularis oris superioris and M. quadratus labii superioris, causing a slight pursing of the upper lip, similar to, but not so strongly marked as in the sound "OO."

And yet we must consider the M. orbicularis oris as being dominant in the upper lip since it is undoubtedly so in the lower. It would be a difficult contortive feat to allow the M. orbicularis oris (i.e. superioris and inferioris) to act in the opposite capacities, the one dominant and the other resistant, and is quite likely to occur in ordinary speech, provided that only the M. orbicularis oris and the labial tractors are functioning.

A slightly different factor is introduced when the M. mentalis acts, for then in the lower lip, both the M. orbicularis oris and the labial tractors are resistant in the new force.

The shape of the upper lip is due partly to its position, but it will be noticed that it has a sharp anterior margin and a flattened labial surface (i.e. the surface which normally is in contact with the other lip). This flattening may well be compared with the labial cords just described. Here the shape of the lip is due to the powerfully acting terminal fibres of the M. quadratus labii superioris, pulling the mucous membrane with its glands upwards, but as the pars marginalis M. orbicularis oris is not in vigorous activity, there is no formation of a true labial cord.

The shape of the lower lip is quite different and here we see the forming of a labial cord due to the activity of the pars marginalis M. orbicularis oris.

The lower lip is brought upwards and slightly inwards so as to be approximated to the upper teeth in such a way that the upper teeth edge lies just posterior to the lower lip red. But here the labial surface is not pitted but rounded, thus showing that the activity of the M. quadratus labii inferioris

and portio labialis platysmae are not great. This is the cushion-like labial cord. The portio peripheralis M. orbicularis oris is dominant and the portio labialis platysmae and M. quadratus labii inferioris resistant, but neither activity is very great.

We now see the M. incisivus inferioris acting vigorously as an anterior stay to the modiolus.

There is evidence of slight activity of the M. mentalis, which again repeats the seeming paradox mentioned in the consonant sound of "B." There is nothing of special note in the return of the lips to the neutral position.

The action of the pars transversa M. nasalis is not well marked in the consonantal portion of the sound.

The Movement of the Facial Muscles in uttering the sound "V" (Table C, 4)

(1) *Consonantal sound (vocal continuous—labial dental)* "*V*." The striking feature here is the early activity of the labial muscles which begin before the fixation of the modiolus. This first movement resembles closely the first part of the sound "OO" and entails a partial pursing of the lips. The M. orbicularis oris on the one hand, and the labial tractors on the other, are acting with such equal intensity that at this stage it is difficult to say which is dominant and which resistant. The only point that makes the M. orbicularis oris seem dominant is the fact that the lips close so as to almost meet, though necessarily anteverted from the teeth. This activity, of course, drags the modiolus forward, but long before it has reached the point necessary for the full pursing of the lips, the modiolus is suddenly and firmly fixed just anterior to the neutral position by the M. zygomaticus and the M. triangularis (three heads).

The lower orbicular muscles still remaining dominant, the lower lip is pressed upwards so that its red lip rests slightly upon the upper incisors, due to the M. mentalis becoming active. During this time the air pressure inside the mouth is increased, thus inflating the buccinator bellows and, in consequence the caput buccale M. triangularis is not seen.

The shape of the two lips is somewhat similar to the consonantal sound "F," and is due to similar muscular activities. But in the consonantal sound "V" there is more pursing of the lips than is the case in the similar sound in "F," and there is in consequence a greater activity of the cruciate modiolar muscles in "V" than in "F." This is the opposite to what has been expected as "F" is classed as a non-vocal and "V" as a vocalised sound. But, as ordinarily pronounced the letters "F" and "V" are really words, the one with a terminal and the other with an initial consonant, and the explanation of the seeming exception is to be found in Table F, 9. In actual speech the muscular activities of "F" will probably be greater than those of "V," e.g. fain and vain—waif and waive.

The air now being expelled, the caput buccale again appears as the M.

buccinator, swelling disappears. The modiolus remains fixed in approximately the same position as before.

As before, both the M. orbicularis oris and the labial tractors are acting with almost equal intensity.

But now the lower lip opens slightly, thus showing that the M. orbicularis oris is really resistant, but so strongly resistant as to keep the lips pursed slightly. The M. mentalis has ceased to act; the slight opening of the lower lip separates it from contact with the upper incisors. The activity of the pars transversa M. nasi is feebly represented.

(2) *Vowel sounds* (*lingual palatal "EE"*). There is now a gradual relaxation of all tension and the labial tractors become definitely dominant and the M. orbicularis oris resistant, and not very active.

The lips therefore part, the upper to show a portion of the upper incisors, the lower to expose not only the teeth but the gums. During this, the modiolus is brought back to the neutral position and fixed there by the caput longum M. triangularis and M. zygomaticus, so that the lips are now not pursed but lie in contact with the teeth and gums.

The rest of the movement resembles the vowel sound in "B."

The Movement of the Facial Muscles in uttering the sound "TWO" (Table C, 2)

Vowel sound (*labial "OO"*) "*TWO.*" The breath explosive consonantal sound "T" is hardly visible due to the necessity of the production of the succeeding sound "OO." There is no return to the neutral position and the movement begins with the mouth moderately widely opened as at the finish of the letter "V." A portion of the usual movement is thereby omitted by the patient. The ridge below the lower lip red is very well marked and also the triangular area between this ridge and the red lip. For the first time, we here find the position of the tongue to be of paramount importance to the production of the sound, but as there is no alteration in the shape of the lips between the first linguo dental consonantal sound of "T" and the later sound "OO," we can consider both together.

The action is very similar to that required for "OO," but the modiolus is fixed earlier and so there is not such marked pouting.

Also the caput buccale M. triangularis is strongly in action and there is no trace of the M. buccinator. The reverse was, of course, the case in "OO," where the pouting was more pronounced.

The muscles visible are:

Modiolar. M. zygomaticus, portio modiolaris platysmae, and the whole of the M. triangularis (three heads).

Dominant. M. orbicularis oris.

Resistant. M. quadratus labii superioris, portio labialis platysmae and M. quadratus labii inferioris.

Nasal. Pars transversa M. nasalis.

THE MOVEMENT OF THE FACIAL MUSCLES IN UTTERING THE SOUND "RIDGE"
(Table C, 8)

This word consists of three portions, being really a vowel between two consonants. The vowel sound is indicated by the unusual pursing of the lips in the formation of the first consonant "R" and virtually turning this sound into one resembling wri ("OO-r-i"). The difference is rather of interest to the teachers of the deaf and dumb, than to the readers of this article. But by comparing Table C, 8 (*c*) with 8 (*b*) subtle differences can be seen in that there is less red lip showing in the upper lip, less pursing in the lower lip and a slight lengthening laterally of the mouth slit or rima oris. In actual speaking, the context would, of course, help, for this class of sound is acknowledged to be difficult for lip readers.

Considering the sound in detail we find

(1) *1st consonantal sound* (*lingual vocal continuous*). This is produced by a marked pursing of the lips and by the action of the tongue approximating the upper alveolus. As in producing the sound "OO," we notice this is brought about by the late fixation of the modiolus and the almost equal action of the dominant M. orbicularis oris and the resistant labial tractors. This fixation of the modiolus is brought about by the M. zygomaticus, capita longum and latum M. triangularis and M. buccinator. The modiolar muscles are seen to act a little earlier than in the word "OO" but not sufficiently strongly to prevent the modiolus being dragged forward, and in the earliest portion of the action the caput buccale M. triangularis takes the place of the M. buccinator. This latter muscle only comes into action as an antimere, when the M. orbicularis oris is very vigorous.

The pars marginalis forms the red lip into two rounded cushion-like labial cords. The pars transversa M. nasalis is seen to be active.

(2) *Vowel sound* (*lingual palatal*) which causes the lengthening of the mouth slit.

(3) *2nd consonantal sound* (*vocal explosive "J" as in Judge*). This sound is produced by the anterior third of the tongue being pressed against the upper alveolus just above the crowns of the central incisors. It represents the sound "G" and its effect is different from any of the previous movements. The first sign of this sound is that the M. orbicularis oris loses its dominant attitude and becomes now strongly resistant to the labial tractors; and also the pursing of the lips disappears.

The modiolus at the same time is dragged just posterior to the neutral position by the modiolar muscles mentioned above, and is then fixed by the M. zygomaticus, capita buccale and longum M. triangularis and portio modiolaris platysmae. There is also some indication of the caput latum M. triangularis being active. But the dominant muscles go on acting very vigorously and the M. orbicularis oris becomes less and less active and soon is very feebly resistant, and we find the upper lip curved upwards and outwards, completely

exposing the upper incisors. At the same time, the lower lip is dragged greatly downwards and more forwards than usual, thus exposing not only the teeth and gums, but also the inferior fornix.

Thus practically the whole of the anterior portion of the vestibule is exposed.

THE MOVEMENT OF THE FACIAL MUSCLES IN UTTERING THE SOUND "WHAT"
(Table C, 7)

(1) *1st vowel sound* (*labial vocal "OO"*), "*WHAT.*" We start here at the end of the sound "two," just as the lips have relaxed but remaining a little pursed.

The pursing now becomes marked once more in a way similar to that seen in the previous word. The lips begin to contract before the modiolus is fixed and, in so doing, drag the modiolus forward. Then the modiolus is fixed by the M. zygomaticus and the M. triangularis (three heads). The caput buccale does not show in the slide, Table C, 7 (*b*). The M. buccinator also acts slightly both as bellows and as an antimere. The portio marginalis M. orbicularis oris makes the red lip margin into labial cords in the way explained previously.

The labial tractors are resistant to the corpus or portio peripheralis M. orbicularis. The lips now meet but do not close completely as a small opening is left for the escape of air and it is during this process that the bellows action of the M. buccinator is noticeable. This is the point selected for Fig. C, 7 (*b*). The muscles now become increasingly active right up to the time of the opening of the lips. The pars transversa M. nasalis is seen to be in action.

(2) *2nd vowel sound* (*lingual short "O" as in box*). Then suddenly the M. orbicularis oris relaxes and becomes resistant and the labial tractors dominant. The M. orbicularis oris superioris and M. quadratus labii superioris regain the neutral state and the upper lip remains in this state. But the inferior labial tractors continue to act vigorously and the lower lip is drawn down and the lower jaw opens. At the same time, the modiolus is drawn back to the neutral position by the cruciate modiolar muscles which become less and less evident as the modiolus approaches the neutral position. The upper lip is maintained in the normal or neutral position, just covering the upper teeth, but the lower lip is dragged down until the lower teeth are exposed to about the same extent as was seen in the vowel sound of "F." The modiolus is fixed during the movement by the M. zygomaticus caninus and caput longum M. triangularis.

The under surface of the tongue is plainly visible, as the tip seeks the alveolar margin in preparation for the next sound (this is not seen in the lantern slides).

(3) *Consonantal sound.* (*Breath explosive, lingual alveolar.*) Next the jaw is closed again until the teeth almost or actually meet.

During this sound the modiolus shows the M. caninus, M. zygomaticus and caput longum M. triangularis and M. incisivus inferioris in activity. The

lower lip is still held down showing the teeth and gum by the dominant inferior labial tractors. But now also, the upper lip is drawn up slightly by the dominant M. quadratus labii superioris, so as to expose slightly the upper teeth. This is understandable when one considers that for the production of the sound, the tongue is pressed against the centre of the upper alveolus just above the crowns of the central incisors and that the high-pitched sound issues between these two surfaces.

THE MOVEMENT OF THE FACIAL MUSCLES IN UTTERING THE SOUND "WHY"
(Table C, 9)

(1) *Vowel sound* (*labial "OO"*) "*WHY*." We begin here at the end of the word "ridge" where the labial tractors are dominant and the M. orbicularis oris fully resistant, and the lips are widely opened.

Now the M. orbicularis oris becomes dominant again, but the labial tractors resist very vigorously and powerfully as in the word "OO." The modiolus also is not fixed but is dragged forward by the dominant M. orbicularis oris.

The resultant, of course, is a true pursing of the lips. When the pursing is almost completed, the modiolus is firmly fixed by the M. zygomaticus, M. triangularis (capita longum and latum) and M. buccinator. It will be again noticed that it is the M. buccinator and not the caput buccale that is acting as an antimere to the vigorously acting M. orbicularis oris. The pars marginalis orbicularis oris forms the lips into labial cords. The pars transversa M. nasalis is seen to be active.

(2) *Vowel sound* (*diphthongal "igh"*). The M. orbicularis oris now becomes resistant and the lips are opened by the labial tractors which are dominant. At the same time the modiolus is dragged back to the neutral part by the M. zygomaticus, M. buccinator and M. triangularis (capita longum and latum). When this position is attained, the modiolus is fixed there by the M. zygomaticus and caput longum M. triangularis. Meanwhile, the upper lip has come to rest covering the upper teeth but the lower jaw is being opened and the lower lip dragged more and more downwards by the dominant inferior labial tractors. Then the muscles acting upon the modiolus change, for the M. zygomaticus apparently ceases to act and the M. caninus portio modiolaris platysmae and caput longum M. triangularis hold the position and this they do to the end of the sound.

WHISTLING

No special slide has been made to represent this, since the facial expression is practically indistinguishable from 8 (*b*), Table C. The muscular activity is very vigorous and the labial cords are well marked. There is also well-marked activity of the pars transversa M. nasalis, similar to that of the sound "OO," but of greater intensity. Though the actual facial expression in whistling is most closely akin to the sounding of "OO" as in Table C, 8 (*b*), yet even this is very little removed from other consonantal sounds, e.g. Table C, 7 (*a*), which

represents the lips opening as the sound "P" issues thereform. One cannot help thinking that a little greater pressure of air in the cavum oris in Table C, 7 (*a*) would both distend the buccinator bellows and give a whistling sound rather than the consonantal sound "P." I understand this is one of the difficulties encountered in teaching deaf-mutes to speak.

Whistling is really nothing more than a continuous non-vocalised consonantal sound. It is a "high-explosive" consonant.

The Movement of the Facial Muscles in "Amusement" (Table C, 9, 10)

Hitherto, the activities described have been purposeful, brought about by the achievement either of speech or of whistling. This has necessitated a great activity of the M. orbicularis oris and a firm fixation of the modiolus. The point of fixation of the modiolus may vary for different sounds, but it must be more or less precise for any particular sound.

Now we are about to consider the activities brought about by amusement, which is an antithesis of purpose, not only psychologically but physiologically. For the secret of laughter is the involuntary complete inhibition and relaxation of the M. orbicularis oris and the absolute lack of fixation of the modiolus. The modiolar movement in laughter, like the emotion it expresses, is a simple and primitive one. In the cinematograph film there were fortunately seen many states of laughter, viz. the true involuntary laughter, the voluntary or forced laughter and the involuntary laughter which the subject succeeded in controlling.

In both smiling and laughter the difference is one of degree only and not due to the activity of additional muscles.

In slide 10 (Table C) we have represented some of these states, viz. smiling, 10 (*a*), repressed smiling, 10 (*c*), laughter, 10 (*b*) and repressed laughter, 10 (*d*). In slide 9 (*c*) we have forced laughter. The first thing that is noticed is that neither in smiling nor in laughter is there any sign of activity of the caput buccale M. triangularis, whereas in forced laughter or when attempting to control smiling or laughing, the caput buccale is well seen. This might be explained, though incorrectly, by applying the axiom that a muscle belly becomes prominent only when there is a resistance to its activity (Table F, 6) and because in smiling and laughing the powerful M. zygomaticus would overcome all resistance; the caput buccale could be active and yet show no sign of its activity. That this is not true is evident by comparing slides 10 (*b*) and 10 (*d*) (Table C), when it will be seen that the M. zygomaticus is equally active in both cases, in fact, it is more powerfully contracted in 10 (*d*) than in 10 (*b*), and yet the caput buccale is only seen in the former. Of course, in 10 (*b*) the caput buccale fibres shorten to adapt themselves to the new position of the modiolus but they do not exert any traction upon the modiolus. The explanation is that in laughter there is little or no resistance offered by the

M. orbicularis oris, which is as completely relaxed as one could expect a muscle to be. This being so, there would be no need for the caput buccale M. triangularis to act. But if the M. orbicularis oris were not completely relaxed from any cause, then we should expect to see the caput buccale called into activity. And such indeed is the case, as will be presently seen in unwilling or repressed laughter. But even supposing the caput buccale M. triangularis were in activity in laughter, its action is but a feeble one and it is no more entitled to be called a muscle of laughter than are the labial tractors. These latter can be shown to play a very definite part in the expression of laughter, and yet no one has ventured to call them the "Lach muskel." Like all other terms that are misleading or wrong, this one will probably be replaced by one more suitable than M. risorius.

Laughter (Table C, 10 (*b*)). The modiolus here is labile and is drawn upwards and outwards by the powerful M. zygomaticus to a degree depending solely upon the natural capacity of the subject and the degree of amusement. The dominant M. zygomaticus is opposed by a very resistant caput longum M. triangularis and the two muscles form a very prominent ridge stretching from the zygoma to the chin. This movement superiorly and laterally of the modiolus, of necessity drags the angle of the mouth superiorly and laterally, and this affects both lips. The position of the upper lip is mainly due to the bi-lateral action of the M. zygomaticus upon the modioli. For if both modioli are simultaneously dragged superiorly and laterally the upper lip must be stretched tightly across the teeth and also dragged superiorly. This stretching of the upper lip across the teeth by the M. zygomaticus, would naturally cause a bellying and bowing downwards in the medial part of the upper lip and it is the straightening out of this bow that is the function of the M. quadratus labii superioris.

The M. quadratus labii superioris is dominant and draws evenly upwards the whole of the upper lip so that it forms practically a straight line exposing the medial teeth as far as the canines and often also the gingiva. This action of the M. quadratus labii superioris is almost unopposed by the M. orbicularis oris, and the muscular lip is drawn up under the fatty envelope and, dragged back like a curtain by the M. zygomatici, the fatty envelope is thrown into a series of folds or creases. Thus the naso-labial fold is deepened but it runs practically in a straight line from the ala nasi to the angle of the mouth.

The centre of the lower lip remains stationary or is perhaps even slightly depressed. Here again, owing to the M. orbicularis oris being relaxed we see no evidence of the labial tractors being contracted but as the red lip is much dragged down, we may safely infer that both the M. quadratus labii inferioris and portio labialis platysmae are in action. This is further borne out by the study of the paralysis of the portio labialis platysmae as seen in Table C, 1 (*b*), (*c*) and (*d*). With the centre of the lower lip held inferiorly and more firmly medially than laterally, and the modiolus dragged superiorly and laterally, the beautiful curve of the lower lip is effected. If we compare the

rima in laughing with the rima in saying the letter "E" (e.g. Table C, 3 (*d*)), we see great similarity in shape; but the whole rima has been dragged upwards in laughing and dragged downwards in saying "E." The lower lip is the more stationary in laughing but the upper lip quite stationary in saying "E."

In the chin region the soft tissues in the middle line have been flattened and forced slightly inferiorly. This is the two-cycle action of the M. mentalis. The cylinder head composed of the M. orbicularis oris and the M. quadratus labii inferioris pushes down the piston and therefore the muscular cylinder wall. At the same time it also flattens antero-posteriorly the piston and cylinder wall.

Also notice the laughing eyes due to the old connection with the pars peripheralis M. orbicularis oculi.

Most interest, however, centres not so much about the expression of amusement as about its counterfeit and its attempted suppression. In forced laughter, Table C, 9 (*c*), and in suppressed smiling and laughing, Table C, 10 (*c*) and (*d*), there is lacking or absent the one essential for true laughter and that is complete relaxation of the M. orbicularis oris. In the former case there is not the involuntary complete inhibition, and in the latter case there is the voluntary contraction of the M. orbicularis oris. And in all three cases we at once notice the great activity shown by the caput buccale M. triangularis. Whether voluntary as in Table C, 9 (*c*) or involuntary as in 10 (*c*) and (*d*), unwilling laughter invokes the aid of the caput buccale M. triangularis to overcome the resistance offered by the M. orbicularis oris and to pull the modiolus laterally.

To take the photos seriatim:

Forced laughter (Table C, 9 (*c*)). Here the voluntary desire to laugh is greater than the involuntary impulse to laugh. Not being a spontaneous and involuntary act there is lacking the usual involuntary inhibition of the M. orbicularis oris. It is this and this only which leads to the detection of these efforts, not only in this subject where the muscular activities are seen, but in other people in whom we see only the results of this altered activity.

As in true laughter, the two main muscles that are visible are the M. zygomaticus and the caput longum M. triangularis. On comparing Table C, 9 (*c*) with 10 (*b*) there seems little to choose in either case between the amount of activity of these muscles. And yet in 9 (*c*) the modiolus is dragged but little laterally and not at all superiorly. To overcome this resistance offered by the M. orbicularis oris, there is now called into play the caput buccale M. triangularis which can help drag laterally the modiolus, but can have no effect in dragging it superiorly. As the modioli are not dragged superiorly the upper lip will not be dragged superiorly nor the upper teeth be exposed. Hence, there will be no need for the M. quadratus labii superioris to act. Of course, it is quite possible that in some cases, the modiolus could be dragged slightly superiorly as well as laterally, but it would never reach the extent of true laughter.

This lack of a movement superiorly of the modiolus, of course, has its effect upon the lower lip in which no sign of curving is to be seen.

This gives to the face a somewhat artificial presentation of laughter, though the wrinkles at the corners of the eyes try to mask this.

Repressed smile and laughter. This is the reverse of the last picture for here the involuntary impulse to laugh is equal to and almost greater than the voluntary desire not to laugh. There is, therefore, a spontaneous and involuntary relaxation of the M. orbicularis oris accompanied by an equally spontaneous activity of the M. zygomaticus. The main voluntary effort is concentrated upon fixing the modiolus as near to the neutral position as possible, and to do this successfully, some voluntary control must be obtained over the M. orbicularis oris. This cannot of course hope to be complete and so it must be assisted in every way that is possible and one may thus get a pyrotechnical display of muscular activity such as is seen in Table C, 10 (*d*).

Repressed smile (Table C, 10 (*c*)). In smiling the degree of amusement is not very great and hence the involuntary relaxation of the M. orbicularis oris has not reached beyond the stage of voluntary control. The tightly compressed and straight lips show that this control has been gained in a measure great enough to obviate the need of much extraneous muscular assistance. This compression of the lips not only hides the teeth, but also inverts the "red lip" so that very little is visible.

The modiolus will be seen to lie posterior and slightly inferior to the neutral position in spite of the activity of the M. zygomaticus. This, to a very large extent, is due to the activity of the M. orbicularis oris preventing the upwards and outwards pull of the M. zygomaticus, though it is greatly assisted in this by the capita latum and longum M. triangularis and the M. incisivus inferioris.

That there is real amusement, and a great though involuntary impulse to express it, is shown by the activity of the caput buccale M. triangularis. This muscle is called into play against the volition of the subject as an adjuvant to the M. zygomaticus in its attempt to drag laterally the modiolus. It is the resistance offered by the M. orbicularis oris to this lateral movement of the modiolus which calls into activity the caput buccale M. triangularis.

Table C, 10 (*d*). This is, of course, an exaggeration of the last picture, but here the impulse to laugh is so great as almost to overcome the will not to laugh, and every modiolar muscle (excepting the M. buccinator) is called in to help one side or the other. The M. orbicularis oris is involuntarily relaxed to such an extent that the subject is unable to overcome this by direct voluntary control and has to resort to various devices to achieve this end. These will be studied presently, but whilst doing this, the other involuntary factors causing laughter will be enumerated. For the sake of clearness, these factors will be studied under two heads, viz.:

(*a*) Modiolar factors or factors influencing the position of the modiolus.

(*b*) Labial factors or factors influencing the position of the lips.

(*a*) *Modiolar factors.* The involuntary factors attempting to drag the modiolus laterally and superiorly are:

First and chiefest, the M. zygomaticus which is seen in the strongest activity.

Secondly, assisting this and attempting to overcome the voluntary resistance of the M. orbicularis oris, we see the caput buccale M. triangularis in activity.

Thirdly, the M. incisivus superioris, which is attempting to drag superiorly the modiolus. It is true that this muscle also tends to drag the modiolus medially and thus assist the M. orbicularis oris, but this effect is much more feeble than its attempt to pull superiorly the modiolus.

Fourthly, the involuntary relaxation of the M. orbicularis oris. To combat this and prevent the superior though not the lateral movement of the modiolus there are:

(1) The powerful contraction of the capita longum and latum M. triangularis.

(2) The voluntary control gained over the M. orbicularis oris.

(3) The extraneous devices used for strengthening the action of the M. orbicularis oris, viz. the M. mentalis which will be considered later.

The result of all this is that the modiolus is fixed lateral and inferior to the neutral position. The inferiority of the position is probably greater than in Table C, 10 (*c*), but this is certainly made to appear greater owing to the bowing cranially of the rima oris.

(*b*) *Labial factors.* The involuntary factors attempting to open the lips are:

(1) The involuntary relaxation of the M. orbicularis oris.

(2) The pull of the superior labial tractors which is great, especially in the median line, as is shown by the small median crescentic fold of the lip red at the inferior edge of the philtrum and the slight upward bowing of the upper lip.

(3) The pull of the inferior labial tractors which is also great for the fibres of both the portio labialis platysmae and M. quadratus labii inferioris are distinctly visible.

To combat this, and prevent the opening of the lips there are:

(1) The voluntary control of the M. orbicularis oris.

(2) The powerful contraction of the pars transversa M. nasalis as is shown by the pinching of the nostrils similarly to that seen in Table C, 6 (*b*). This probably acts by association; for just as a powerful contraction of the M. orbicularis oris seems to cause a like powerful contraction of the pars transversa M. nasalis, so this contraction, which is really an indication of the amount of voluntary effort that is being made to control the M. orbicularis oris, may possibly help to increase the contraction of the M. orbicularis oris.

(3) The contraction of the M. mentalis which is very powerful. This not only effectually prevents the lower lip from being dragged downwards but also pushes it directly upwards firmly against the slightly retracted upper lip and prevents the teeth from being exposed. In addition to this, the action of

the M. mentalis, inferior labial tractors and M. orbicularis oris, make the lower lip into a semi-rigid body which is an additional hindrance to the movement of the modiolus laterally.

The result of these activities is to cause a facial expression so very unlike that of amusement or laughter but closely simulating Duchenne's figure expressing discontent (or contempt?).

CONCLUSION

In conclusion, I should like to give thanks to all those who have assisted in the production of this article. To Dr Huber of the Johns Hopkins Medical School, for his private letter, giving, in advance of publication, his ideas with regard to the origin of the different muscles and also for copies of his own more recent articles; to the Anatomy Department of the University of Sydney, for the supply of material; to Prof. Hunter of that Department, for assistance and advice and also for revising the MSS.; to Drs Burkitt and Coen, also of that Department, the former for the initial work we did together and the works of reference he collected, and the latter for pointing out to me that the pars transversa M. nasalis was in activity during the production of certain sounds, and to all the members of the staff of that Department, and especially to Mr Schaeffer for the preparation of lantern slides from the film; Messrs Bagnall and Newson for the cutting of sections of lips, and Mr Burfield for the microphotographs.

I am also indebted to H. Earlam, Esq., of the Blind, Deaf and Dumb Institution of this city for the preparation of Table E and for assistance in the classifications of sounds, and lastly to the Australian Pictures, Ltd, for the use of the orthoscope and other material essential for the dissection of the film.

Table A. *Table of the muscles that are described*

1. M. malaris (pars peripheralis M. orbicularis oris).
   - (*a*) Caput mediale.
   - (*b*) Caput laterale.
2. M. nasalis.
   - (*a*) Pars transversa.
   - (*b*) Pars alaris.
3. Musculi circum. orem.
   - A. Musculi quadrati labii.
     - (1) M. quadratus labii inferioris.
     - (2) M. quadratus labii superioris.
       - (*a*) Caput angulare.
       - (*b*) Caput infraorbitale.
       - (*c*) Caput zygomaticum.
   - B. Platysma.
     - (1) Nape platysma.
     - (2) Neck platysma.
       - (*a*) Pars aberrans.
       - (*b*) Pars labialis.
         - (*a'*) Portio modiolaris.
         - (*b'*) Portio labialis (portio labialis proprius).
         - (*c'*) Portio mandibularis.

Table A (*continued*)

C. Musculi modioli.
  (1) Musculi cruciati.
    (*a*) M. zygomaticus.
    (*b*) M. caninus.
    (*c*) M. triangularis.
      (*a'*) Caput buccale.
      (*b'*) Caput latum—caput transversum.
      (*c'*) Caput longum.
  (2) Musculi transversi.
    (*a*) M. buccinator.
    (*b*) M. orbicularis oris.
D. Musculi accessorii.
  (1) Pars nasalis M. orbicularis oris.
  (2) M. incisivus superioris.
  (3) M. mentalis.
  (4) M. incisivus inferioris.

Table B. *Table of movements executed by the subject, Miss X*

1. Making the following sounds:
   B, F, M, OO, P, V, Two, What, Ridge, Why.
2. Reflection and attention.
3. Anxiety, grief, despair, pain.
4. Contempt, disgust.
5. Unpleasant surprise, fear.
6. Hatred, anger, aggression.
7. Pleasant surprise, smiling, laughing.
8. Facial movements, starting at the forehead and proceeding downwards:
   (*a*) Wrinkling of forehead and frowning.
   (*b*) Closing eyes very tightly.
   (*c*) Screwing up nose.
   (*d*) Making a long upper lip.
   (*e*) Pursing the lips.
   (*f*) Raising the chin.
9. Whistling.
10. Reading aloud.

Owing to the film sticking when the subject had got as far as closing the eyes very tightly (Table C, 8 (*b*)) it was found necessary to repeat again the movements 5, 6 and 7, as it was feared the film might have been fogged in the effort to free it.

The first effort at laughter was a very spontaneous and hearty effort, whereas the second attempt in the second film was rather forced. This, however, was a very useful contrast and will be shown to be due to different muscular action.

As was to be expected much of the film was a failure for some of the emotions were but poorly reproduced. But as against this, the occasional lapses were of extreme value, especially when, on one occasion, the humour of the situation overcame her and she made desperate efforts to control her amusement (Table C, 10 (*c*)). It was a great fortune to find in one person a physical defect of this rarity combined with a high degree of intelligence, good culture and very clear and distinct enunciation.

[Table C has been put after Table F.]

Table D. *Classification of sound*

This is a classification of the different kinds of sounds used in ordinary speech and was compiled for me by H. Earlam, Esq., Superintendent of the Deaf, Dumb and Blind Institution in this city.

Its terminology has been used in describing the various portions of the sounds analysed.

Vowel sounds:

Basic	AR	(bar)	
Semi-basic	ER	(fur)	
Labial	AW	(saw)	Lengthening of the cavum oris to a tube
	OO	(boot)	
	OO	(look)	
	W	(was)	
Lingual palatal	A	(bat)	Placement of the tongue—essential mouth opening—secondary
	E	(bet)	
	EE	(seed)	
	I	(bit)	
Lingual	O	(box)	
	U	(but)	
Diphthong	OW	(a—oo)	
	OY	(aw—i)	
	AY	(e—i)	
	IGH	(ar—i)	
	EW	(i—oo)	
	OA	(e—oo)	

Consonantal sounds:

Basic breath	H				
Breath explosive ...	P	T	Ch	K	
Vocal explosive	B	D	J	G	
Nasal vocal	M	N		Ng	
Breath continuous ...	F	Th (pith)	S	Sh	
Vocal continuous ...	V	Th (that)	Z	Zh (measure)	
Lingual vocal continuous	L	R			

Table E. *Analyses of sound*

This table was compiled for convenience of reference.

It represents the muscular activities during the crucial moments of each sound recorded.

These are depicted in the various lantern slides.

It does not attempt to give any of the intermediate stages in passing from one crucial moment to another. A description of these had been given in the text, but they cannot be appreciated without seeing the actual cinematograph film.

The various numbers given with each portion of the various sounds represent the number of inches of the film devoted to that portion of the sound.

The rate of the film was 4 feet per second, which was four times the rate of an ordinary film.

The time taken for each movement can therefore be easily calculated.

Another way of expressing this is that the cinema took sixty-four photos per second and when it is remembered that often the visibility of a muscle is limited to three or four photos, it will be seen that 1/16th to 1/20th of a second may be calculated as an apparently ordinary rate of contraction for the facial muscles. But these calculations are not based upon distinct and slow speech, so that in ordinary speech the time must be lessened and in rapid speech the muscular contractions still more brief.

These figures are much at variance with the contraction time of a muscle twitch as given by Halleburton; but it must be remembered that in this article when the contraction of a muscle is

Table E (*continued*)

spoken of, it is really only the period of visibility that is being calculated. But apart from consideration of the action of any particular muscle, we have other less equivocal facts on which to base some idea with regard to the duration of a muscular contraction. Taking the letter "B" as an example, we find that the complex consonantal sound is begun and completed in about half a second and that it is followed by another sound requiring a different muscular combination. The movement is a slow and deliberate one, and the different muscles involved in the consonantal sound are not acting for the whole of this half-second, so that in ordinary speech the action of the facial muscles must resemble rather a series of muscular twitches than of an ordinary muscular contraction. It seems indeed extraordinary that such precision can be obtained in this manner, and one must conclude that the facial muscles are in some ways different from the ordinary musculature of the body. In this respect it is interesting to reflect that they may have been derived from the panniculus carnosus which in lower animals is merely a twitching muscle.

Analysis of Sounds

Neutral position		Modiolus:	M. zygomaticus caput longum.
	Lips.	Dominant:	inferior labial tractors.
		Resistant:	M. orbicularis oris inferioris.
		Labial consonant 30″	
B		Modiolus:	M. zygomaticus portio modiolaris.
			M. triangularis (three heads).
	Lips.	Dominant:	M. orbicularis oris, M. mentalis.
		Resistant:	labial tractors.
		Nose:	pars transversa.
		Vowel 26″	
B.		Modiolus:	M. zygomaticus caput longum.
	Lips.	Dominant:	labial tractors.
		Resistant:	M. orbicularis oris.
		Labial consonant 33″	
		Vowel 42″	
P	The muscular activities were similar to B.		
		1*st consonant* 18″	
WHAT		Modiolus:	M. zygomaticus.
			M. triangularis (three heads).
	Lips.	Dominant:	M. orbicularis oris.
		Resistant:	labial tractors.
		Nose:	pars transversa.
		Vowel 19″	
		Modiolus:	M. caninus.
			M. zygomaticus caput longum.
	Lips.	Dominant:	labial tractors.
		Resistant:	M. orbicularis oris.
		Linguo-alveolar consonant 26″	
		Modiolus:	M. caninus.
			M. zygomaticus caput longum.
			M. incisivus inferioris.
	Lips.	Dominant:	labial tractors.
		Resistant:	M. orbicularis oris.
		Vowel 39″	
F		Modiolus:	M. caninus, caput longum, portio modiolaris.
	Lips.	Dominant:	labial tractors.
		Resistant:	M. orbicularis oris.

Table E (*continued*)

		Dento-labial consonant 29″	
F		Modiolus:	M. caninus.
			M. zygomaticus.
			M. triangularis (three heads).
			M. incisivus inferioris and portio modiolaris.
		Bellows:	M. buccinator.
	Lips.	Dominant:	M. orbicularis oris, M. mentalis.
		Resistant:	labial tractors.
		Nose:	pars transversa.
		Dento-labial consonant 30″	
V		Modiolus:	M. zygomaticus.
			M. triangularis (three heads).
	Lips.	Dominant:	M. orbicularis oris, M. mentalis.
		Resistant:	labial tractors.
		Nose:	pars transversa.
		Vowel 52″	
		Modiolus:	M. zygomaticus caput longum.
	Lips.	Dominant:	labial tractors.
		Resistant:	M. orbicularis oris.
		1*st vowel sound* 33″	
M		Modiolus:	M. caninus, caput longum, portio modiolaris.
	Lips.	Dominant:	labial tractors.
		Resistant:	M. orbicularis oris.
		Labial consonant 17″	
		Modiolus:	M. zygomaticus.
			M. triangularis (three heads).
			M. incisivus superioris.
	Lips.	Dominant:	M. orbicularis oris, M. mentalis.
		Resistant:	labial tractors.
		Nose:	pars transversa.
		Period of relaxation 7½″	
		Modiolus:	M. zygomaticus.
			M. triangularis (three heads), portio modiolaris.
	Lips.	Dominant:	labial tractors.
		Resistant:	M. orbicularis oris.
		71″	
OO		Modiolus:	M. zygomaticus, capita longum and latum.
			M. buccinator.
	Lips.	Dominant:	labial tractors.
		Resistant:	M. orbicularis oris.
		Nose:	pars transversa.
		Linguo-alveolar vowel 37″	
RIDGE		Modiolus:	M. zygomaticus, capita longum and latum.
			M. buccinator.
	Lips.	Dominant:	labial tractors.
		Resistant:	M. orbicularis oris.
		Nose:	pars transversa.
		Linguo-alveolar consonant 25″	
		Modiolus:	M. zygomaticus, capita longum and buccale (? latum).
	Lips.	Dominant:	labial tractors.
		Resistant:	M. orbicularis oris.

Table E (*continued*)

Labial consonant 54″

WHY		Modiolus:	M. zygomaticus, capita longum and latum.
	Lips.	Dominant:	M. orbicularis oris.
		Resistant:	labial tractors.
		Nose:	pars transversa.

Vowel 22″

		Modiolus:	M. caninus, caput longum, portio modiolaris.
	Lips.	Dominant:	labial tractors.
		Resistant:	M. orbicularis oris.

70″

TWO	Similar to OO.

Table F. *Axioms of muscular action*

1. The action of any facial muscle is always balanced or controlled by an antimere; one paramere being dominant and the other resistant. The same is true of groups of muscles.

2. The sequence rather than the strength of antimeric action often decides the facial expression.

3. The position of the modiolus determines the form the lips take due to the action of the M. orbicularis oris. If the modiolus is fixed and posterior the lips cannot be pursed though they may be separated from the teeth and slightly everted; if the modiolus is fixed and anterior the lips may be pursed.

4. If the M. orbicularis oris is dominant many muscles are required to fix the modiolus; but if the M. orbicularis oris is resistant, the modiolus may be fixed by the action of the even two muscles, e.g. M. zygomaticus and caput longum M. triangularis.

5. Many of the facial muscles possess the power of acting in sections. One part may be quiescent or in mild contraction, whilst the other is acting vigorously. This is best exemplified by the M. triangularis and platysma but is also seen in other muscles, e.g. M. quadratus labii superioris.

6. The prominence of a muscle belly depends not only upon the contraction of that muscle but also upon the strength of the antimeric opposition.

7. If for any reason the distal portion of a muscle becomes separated or partially separated from its corpus and acts as a separate entity, then this distal portion may show a great increase in the size and number of its fibres and may even acquire a different innervation.

8. Vocalised sounds require less activity and effort of the facial muscles than unvocalised, and vowel less than consonantal sounds. In other words, in the production of sound, the laryngeal and labial muscles to some extent are complementary, i.e. the vocal and labial cords are to some extent complementary.

9. A consonantal sound when it terminates a word requires less muscular activity than the same consonantal sound when it begins a word; in the former there is the realisation that there is no succeeding sound to make, and in the latter there is the anticipation of the succeeding sound.

Table C. *Table of lantern slides, diagrams, photographs and dioptographic tracings*

This table has been compiled to show the reader at a glance the chief point of interest for which each particular slide was made.

There is no attempt to describe in detail all the muscles shown though each picture necessarily exhibits many points of interest other than those specifically mentioned for that picture; but such points will be equally well, perhaps much better, illustrated in some other picture. All that is claimed is that there is no point of interest that is not mentioned in some picture and this the reader can again appreciate in other pictures.

The slides are arranged in groups of four pictures and the reading is from left to right, taking the two top pictures first and then the two bottom ones. In referring to these pictures, they will be called (*a*), (*b*), (*c*) or (*d*), according to their position, e.g. the vowel sound of "V" will be alluded

Table C (*continued*)

to as 4 (*d*) or more usually this will be prefixed by the number of the table and be alluded to as Table C, 4 (*d*).

The numbers in brackets allude to the different numbers in Table B, which refer to the different movements performed by the subject, e.g. in 10 (*d*) we see the number 4 in brackets and this means that this emotion was culled from the fourth movement attempted by the subject when she was overcome with amusement and tried to control it.

The capital letters in brackets indicate that the picture has been taken from some portion of the film whilst the subject was saying that particular sound.

The smaller letters simply allude to the subdivision of Table B, 8. As has been mentioned the film was taken in two portions and whilst the machine was speeding up there was a period during which the subject was not attempting to produce any sound or any movement. Any picture taken from this quiescent period will be labelled i—ii.

6 (*c*), (*d*) and 7 (*a*) are three consecutive photos in the film to show the opening of the labial cords. A few of the pictures, however, deserve more mention than has been given in the table or in the subsequent letterpress and they will be given in detail here:

2 (*a*). In this picture, though the general expression is good, the lips are apart. The M. zygomaticus, however, is generally visible when the face is in repose.

11 and 12. Show different modes of fixing the modiolus.

Lantern Slides (culled from the Cinematograph Film)

1. (*a*) Scar on side of the neck of Master O. A.
   (*b*) Normal expression of Master O. A.
   (*c*) Smiling „ „
   (*d*) Laughing „ „
2. (*a*) Normal expression of Miss X (8–9).
   (*b*) Neutral position (B).
   (*c*) To show visibility of parotid duct (F).
   (*d*) To show angulo marginal band (Two).
3. Different phases in the pronunciation of the sound "B":
   (*a*) Early opening.
   (*b*) Meeting of the lips to form labial cords (consonantal sound).
   (*c*) Ditto (a later stage).
   (*d*) Vowel sound.
4. Different phases in the pronunciation of the sounds "F" and "V":
   (*a*) Vowel sound of "F."
   (*b*) Consonantal sound of "F."
   (*c*) „ "V."
   (*d*) Vowel sound of "V."
5. Different phases in the pronunciation of the sound "M":
   (*a*) Vowel sound of "M."
   (*b*) Transition stage.
   (*c*) Consonantal sound of "M."
   (*d*) Period of relaxation.
6. The formation and relaxation of labial cords as illustrated in the consonantal sound of "P'
   (*a*) Meeting of the lips.
   (*b*) Labial cords well formed.
   (*c*) „ just before the lips open.
   (*d*) „ just as the lips open (photograph immediately following C, 6 (*c*)).
7. Labial cords (*cont.*) and the different phases in the pronunciation of the sound "What"
   (*a*) Labial cords as lips open in the consonantal sound "P" (photograph immediately following C, 6 (*d*)).
   (*b*) First consonantal sound of "What."
   (*c*) Vowel sound of "What."
   (*d*) Second consonantal sound of "What."

Table C (*continued*)

8. Different phases in the pronunciation of the sounds "OO" and "Ridge"
   (*a*) Early stage of sound OO, modiolus forward but unfixed.
   (*b*) Later " " fixed.
   (*c*) First consonantal sound of Ridge.
   (*d*) Second " "
9. Different phases in the pronunciation of the sound "Why," etc.:
   (*a*) Consonantal sound of "Why."
   (*b*) Vowel sound of "Why."
   (*c*) Muscular action in forced laughter (7 in second film).
   (*d*) To show the M. caninus (F).
10. The muscular action in laughter:
   (*a*) Smiling (7 in second film).
   (*b*) Laughter (7 in first film).
   (*c*) Suppressed smiling (4).
   (*d*) Suppressed laughter (4).
11. Different methods of fixing the modiolus:
   (*a*) M. zygomaticus and caput longum M. triangularis (i—ii).
   (*b*) M. zygomaticus, caninus and incisivus inferioris and caput longum M. triangularis (i—ii).
   (*c*) M. zygomaticus and capita longum and latum M. triangularis (What).
   (*d*) Same as 11 (*c*) and in addition the M. buccinator (OO).
12. (*a*) Same as 11 (*c*) and in addition the caput buccale (B).
   (*b*) Same as 12 (*a*) and in addition the portio modiolaris platysmae (Why).
   (*c*) Same as 12 (*a*) and in addition the M. caninus (B).
   (*d*) Same as 12 (*c*) and in addition the M. incisivus superioris and portio modiolaris platysmae (P).
13. A series of pictures to demonstrate the activities of certain muscles.

(*a*) Moderate resistant action of the M. quadratus labii superioris. Notice the obliteration of the cephalad portion of the naso-labial fold (P).

(*b*) Dominant action of caput angulare M. quadratus labii superioris (B, 8 (*c*)). Notice the dragging upwards of the superior end of the naso-labial fold which throws into prominence the nasal portion of the naso-buccal gyrus. The lower end of this appears as a transverse ridge across the nose just superior to the naso-labial fold and might be mistaken as being due to the activity of the pars transversa M. nasalis. It is this dragging upwards of the naso-buccal gyrus which causes the ridges at its upper border and which run obliquely across the bridge of the nose. Also notice very well marked the fibres of the angular head which go to the alae nasi. These are in vigorous activity and help to expand the alae nasi. They are seen as a short longitudinal band appearing beneath the naso-buccal gyrus and ending in the ala nasi. In addition notice the longitudinal ridges in the upper lip and the small crescentic folding of the "red lip" just below the philtrum. The most lateral of these ridges is due to the activity of the infraorbital head of the M. quadratus labii superioris, but the most medial is probably due to the activity of the labial portion of the caput angulare and the crescentic folding of the "red lip" is probably mainly due to this also. Compare with 14 (*a*).

(*c*) Vigorous resistant action of the three heads of the M. quadratus labii superioris during the formation of labial cords and the modiolus fixed close to the neutral position (cf. with 13 (*a*)) (P). The M. incisivus superioris is shown as a ridge across the upper lip stretching from the modiolus towards the ala nasi.

The pars transversa M. nasalis activity is denoted by the "pinching" or "flattening" of the nose superior to the ala nasi. There is also some latero-medial flattening of the ala nasi superiorly. This action is best appreciated by comparing the nose in this photo with 2 (*a*).

(*d*) Showing the dominant activity of the M. quadratus labii superioris (B, 8 (*b*)). Notice that the naso-labial fold is clearly seen in this photo and in 13 (*b*). Notice also the updrawing of the outer third of the upper lip (cf. 14 (*a*)).

14. (*a*) This is the nearest attempt to a "canine snarl" (B, 4). In this probably all three heads of the M. quadratus labii superioris are in different degrees of activity. The caput angulare raises

Table C (*continued*)

the upper end of the naso-labial fold. As these fibres are inserted into the naso-labial fold inferior and posterior to the naso-buccal gyrus, their activity will have the effect of deepening the naso-labial fold. The caput buccale is probably chiefly responsible for the raising of the outer third of the lip, though assisted by the outer fibres of the caput infraorbitale.

(*b*) This shows the actual fibres of the M. mentalis standing out in bold relief (M). Notice that the uppermost fibres can be seen on the left as well as the right side and that the two form a definite horseshoe-shaped muscle.

(*c*) Extreme resistant activity of the M. quadratus labii superioris and zygomaticus (B, 8 (*c*)). The muscles here appear as definite ridges, three for the M. quadratus labii superioris and one for the M. zygomaticus. The condition has already been alluded to. Also notice the definite medial margin of the M. quadratus labii inferioris and that the two muscles meet in the middle line at the red lip margin but not inferior to this. This is merely an exaggeration of the condition observed in C, 8 (*b*).

(*d*) Shows the M. mentalis in a state of strong contraction (B, 8 (*f*)). Notice the cylinder and piston activity of the M. mentalis and the elevation of the surface caused thereby. Also notice that the lower lip is forced upwards and slightly forwards.

13 and 14. From the study of these photographs, it will be noticed that during the activity of the M. quadratus labii superioris the naso-labial fold is sometimes completely obliterated in its upper portion by the prominent body of the muscle, and at other times the naso-labial fold is very well marked and no muscular action is visible. This can be best explained by Table F, 6. For in those cases where the muscle belly is very prominent and obliterates the naso-labial fold the M. quadratus labii superioris is resistant and not dominant and the strength of the activity of the muscle is indicated by the prominence of its muscle belly. But in spite of its very great activity, it is unable to overcome the dominant action of the M. orbicularis oris. Whereas, when the naso-labial fold is well seen and there is no muscle belly visible, the M. quadratus labii superioris is dominant and evidently meeting but little resistance from the M. orbicularis oris. In this case, as we have also seen in the case of the M. quadratus labii inferioris, there is not likely to be any prominence of the muscle belly. The other point that seems probable is the action in sections of the caput angulare M. quadratus labii superioris. The caput has three types of fibres: (*a*) those to the ala nasi; (*b*) those to the lip; (*c*) those to the naso-labial fold. These may act simultaneously but the activity of one set quite overshadows the other two. Whether one set may act quite independently of the other two cannot be definitely stated, but it seems probable. Those fibres going to the ala nasi must often be quite in obeyance. Again compare photographs 13 (*a*) and 13 (*c*) and 14 (*c*), the lip fibres are in a state of greater or less activity but there is no sign of any activity of those fibres going to the naso-labial fold. It is true they might be active and yet show no sign of their activity but one cannot see in these cases that any useful purpose could be served by their activity.

15. (*a*) Shows very clearly the M. incisivus inferioris (7 in first film).

(*b*) Shows the normal pars marginalis M. orbicularis oris.

(*c*) Shows the pars marginalis M. orbicularis oris being dragged downwards by the labial tractors and the consequent delineation of the outline of the pars peripheralis M. orbicularis oris inferioris (F).

(*d*) Shows the pars marginalis formed into cushion-like labial cords, especially the pars marginalis inferioris (Two).

Diagrams

* An asterisk means that the figure is not reproduced.

16. Schematic representation of the surface view in Miss X of the M. quadratus labii superioris, M. triangularis, M. caninus, M. zygomaticus and M. quadratus labii inferioris. The M. orbicularis oculi is shown conventionally and the portio labialis platysmae as though cut across.

17. Schematic representation of the surface view in Miss X of the M. nasalis, M. caninus, pars labialis platysmae (cut across), M. mentalis and the M. incisivi.

*18. Schematic representation of the surface view in Miss X of the M. nasalis, M. incisivus superioris, M. incisivus inferioris and M. mentalis.

*19. Schematic representation of the insertion into the skin of the upper lip and of the origin

Table C (*continued*)

and relations of the M. quadratus labii superioris in H.B. 1, as shown in a sagittal section of the head lateral to the ala nasi.

20. Schematic representation of the pars marginalis and pars peripheralis M. orbicularis oris, M. quadratus labii inferioris and M. mentalis (showing fibrous pad and subjacent bursa).

*21. Camera lucida drawings of sections of the upper and lower lips in D.B. 2.

22. Diagram of a section of the upper lip when at rest.

23. Diagram of a section of the upper lip during the formation of a labial cord.

24. Composite diagram showing the upper lip when at rest and when forming a labial cord.

22, 23, 24. In these diagrams the pars marginalis is roughly triangular in section and slightly larger in circumference than the bundles of the pars peripheralis. Together they form a complete hook-like muscle. The M. quadratus labii superioris fibres are shown penetrating the pars peripheralis but not the pars marginalis. The superficial fibres of the M. quadratus labii superioris are deep in the lip near the fornix, then sweep gradually to the corium where relays enter and then turn abruptly round and sweep between the pars marginalis and pars peripheralis to reach the sub-mucosa. The deeper fibres remain closely applied to the anterior surface of the pars peripheralis and through this muscle relays keep passing to reach the sub-mucosa. During the formation of labial cords, the pars marginalis is shown pressing downwards and probably broadening cephalo caudally. Its superior margin is more or less fixed by the skin fibres of the M. quadratus labii superioris and its inferior margin resisted by the second group of fibres of the same muscle. This descent of the pars marginalis forms the true labial cord and its activity drags slightly downwards the pars peripheralis at its anterior end, thus slightly straightening out the curve of the hook. But the labial cord would be a poor speaking instrument were it not for the activities of the deeper fibres of the M. quadratus labii superioris which drag superiorly the posterior bulging sub-mucous tissues and thus form a comparatively delicate organ of the lip.

25. Diagram of a section of the upper lip of a female chimpanzee.

26. Diagram of a section of the lower lip of a female chimpanzee.

25 and 26. Both these sections show a remarkable likeness to the sections of the human lip. But the labial tractors are better developed in both lips and the M. orbicularis oris is not yet sharply differentiated into a pars marginalis and pars peripheralis. In both sections, however, the preterminal bundles of fibres of the M. orbicularis oris show an increase in size as viewed in these sections. This increase in size was much more marked in the upper than in the lower lip. (Unfortunately, the specimen was too hard to permit of dissection as it had been in formalin for about 15 years.) Also the fibres of the labial tractors penetrated into or through the bundles of the M. orbicularis oris in both lips throughout the whole length of the section right up to the tip. The penetrating fibres near the free margin of the M. orbicularis oris were, however, smaller in size than those penetrating the corpus of the muscle. This was especially true of the lower lip. This was in marked contrast to the human lip for no fibres of the labial tractors were seen to pierce the pars marginalis in the human subject. Another very important point shown in the diagrams were the relative amount of turning over of the marginal fibres of the M. orbicularis oris. The upper lip is, in this respect, very primitive and shows no hook formation but merely a very slight curving with the concavity anterior. This straight and undifferentiated M. orbicularis oris and the fully developed labial tractors may be taken as a type of primitive lip used merely for the prehension of food. The lower lip is, however, much less primitive and may be taken as the type of lip for early speech or in the stage immediately preceding speech. It shows the well-marked hook-like formation of the M. orbicularis oris but true speech is hindered in two ways: firstly, the marginal fibres of the M. orbicularis oris are still closely bound to the corpus of the muscles and could not attempt any individual freedom of movement, and secondly, it is far too intimately related to the labial tractors. These two lips seem to bear out the contention that the pars marginalis is really a speech modification and also that the unciform shape in part is due to the pull of the labial tractors on a relative weakening of the marginal fibres of the M. orbicularis oris. With regard to the marked differences in the uniform formation in the upper and lower lips, it may be remarked here that similar differences were observed in the lips of the adult and foetal human beings examined. And, if the hypothesis of the pars marginalis being a speech modification be correct, it is only natural that this should be so. The lower lip only is essential for labial speech and the place of the upper lip can be, and often is, taken by the teeth. This not only includes

Table C (*continued*)

such sounds as "F' and "V" where this is normally the case, but also sounds like P, B, M and N. The result may not be so cosmetic but it is equally efficient.

27. Diagram of the attachment of muscles to the anterior portion of the mandible (cf. with Spaltcholz). The most noticeable feature is the comparatively bare area surrounding the foramen mentale. With regard to the insertion of the caput longum, it is shown as arising from the tuberculum mentale, and the dotted lines extending both medially and laterally indicate the possible extensions of the origin of this head. The other two capita necessarily are not represented.

28. Diagrams of the basis modioli in three subjects showing their shape, sizes and the attachments of the various muscles. Of necessity these can be only generalisations. Medially, superiorly and inferiorly the boundaries are more or less definite but laterally the boundary is arbitrary, owing to the very intimate connection between the M. buccinator and the mucous membrane of the cheek and basis modioli. There are two cornua or portions projecting into the lips and a basis modioli. The superior cornu is from 0·6 cm. to 1·5 cm. medial, and 1·5 to 1·65 cm. superior to the angle of the mouth. The inferior cornu is from 0·3 to 0·5 cm. medial and 2·0 to 2·5 cm. inferior to the angle of the mouth. These measurements were made from horizontal and vertical lines drawn through the angle of the mouth, as shown in (*a*). The apex modioli was in all cases about 1 cm. lateral to the angle of the mouth and almost on the same horizontal plane. The lateral margin of the basis modioli was supposed to be 1·5 to 2 cm. lateral to the apex modioli. Each of the modioli represented will be described in a manner similar to that used for the lantern slides.

(*a*) Represents the shape of the basis modioli in H. B. 1. Notice the cornu and the labial glands running obliquely across the inferior cornu. These glands do not interfere so greatly with the muscle insertions of the other subjects, owing to the slightly different shape of the inferior cornu.

(*b*), (*c*) and (*d*). Represent the basis modioli of H. B. 1, Nos. 2317 and 2325 respectively. They also show the positions of the insertions of the different muscles into the basis modioli. These are represented by numbers and the key is as follows:

(1) Pars marginalis superior and inferior.
(2) Pars peripheralis superior.
(3) Pars peripheralis inferior.
(4) M. incisivus superior.
(5) M. incisivus inferior.
(6) M. zygomaticus.
(7) M. caninus.
(8) M. triangularis.
(9) M. buccinator.

29. Of a young adult male showing the modiolus in the living subject.

30. Of an adult female Australian aboriginal and her eight months infant, showing the gyrus naso-buccalis in the living subject.

*31. Of an elderly male to show the curtain-like foldings of the panniculus adiposus of the face.

*32. Of two elderly females to show facial wrinkles.

Photomicrographs

33. Of a section of the upper lip of No. 2317 taken just below the ala nasi. This shows the distinction between the pars marginalis and pars peripheralis of the M. orbicularis oris. It also shows remarkably well the termination of the fibres of the M. quadratus labii superioris which are cut longitudinally for a large portion of their course. It should be compared with diagram 23.

34. Of a section of the upper lip of an eight months foetus of European origin. The distinction between the two portions of the M. orbicularis oris is very well shown in this specimen. For the most part the fibres of the M. quadratus labii superioris are cut transversely, though a large bundle cut longitudinally is seen passing between the pars marginalis and pars peripheralis M. orbicularis oris, and another large bundle also cut longitudinally passing between the bundles of the M. orbicularis oris. The great difference between this section and the previous one is the relatively large size of the M. quadratus labii superioris. In this section, the whole of the space between the corium and the M. orbicularis oris is filled by cross-cut bundles of the M. orbicularis oris with a moderate sprinkling of masses of fat and connective tissue.

Dioptographic Tracings

35. Of the facial muscles of H. B. 1 (full face).

36. Of the facial muscles of H. B. 1 (side face).

The capita laterale and mediale of the pars peripheralis M. orbicularis oculi more or less completely hide from view the M. quadratus labii superioris and M. zygomaticus. Notice the very

Table C (*continued*)

large lateral portion of the caput mediale which crosses superficial to the caput laterale to end in the lower end of the naso-buccal gyrus. The M. triangularis. The caput longum is well developed and in the tracings it looks as though there were also a caput transversum present. This was merely a pseudo caput transversum as already explained. The caput latum is poorly developed but shows definite short fibres anterior to the caput longum. The caput buccale is poorly developed.

37. Of the facial muscles of D. B. 2 (full face).

38. Of the facial muscles of D. B. 2 (side face).

The caput laterale of the pars peripheralis M. orbicularis oculi was again well-developed but the caput mediale was much more irregular. The more lateral fibres of this caput end as in H. B. 1 but the more medial fibres end superior to the ala nasi. They are, however, directly continuous with the fibres of the M. depressor capitis supercillii and a few of the most medial seem to act as a procerus nasi. The M. triangularis has not been fully investigated. The caput buccale had a well-marked tendon of origin. The fibres of the caput latum medial to the caput longum were not so well developed as in H. B. 1 and are not shown in the diagram.

39. Of the facial wrinkles of No. 2317.

40. Of the panniculus adiposus of the face in No. 2317.

The dotted areas represent the presence of thick connective tissue and the sagittal (vertical) lines, fat. The fat thicknesses vary as the closeness of the lines. In some areas the fat is accompanied by dense connective tissue and in these areas both dots and lines are present.

41. Of the facial muscles of No. 2317 (full face).

The pars aberrans platysmae has been removed on both sides. On the left side the pars peripheralis M. orbicularis oculi has been removed; on the right side the medial portion of the caput laterale only has been removed. On both sides the capita ended in the naso-buccal gyrus and more or less hid from view the other muscles in this region, the caput laterale covering the M. zygomaticus and caput zygomaticum, and the caput mediale partially covering the capita angulare and infraorbitale. Both capita were easily separated and distinct from the underlying muscles. The caput mediale was not well developed and did not cross the caput laterale. The M. quadratus labii superioris; the caput angulare fibres which were inserted into the naso-labial fold covered and hid from view the labial fibres. This is usual. The caput zygomaticus was divided into a superficial and a deep portion and between these two lay the angular vein. The deep portion joined the M. quadratus labii superioris. The superficial portion ended in the naso-buccal gyrus. The M. zygomaticus divided into a superficial and deep portion as usual. Some of the superficial fibres ended in the cheek. The M. triangularis will be shown more fully in the next tracing. Most of the muscle has been removed upon the right side to show the portio labialis platysmae fibres.

42. The modiolus on the right side of face of No. 2317.

The pars aberrans platysmae is divided across the lower portion of the M. buccinator. The M. caninus is shown passing between the superficial and deep portions of the M. zygomaticus. In this case the M. incisivus superioris does likewise. The difficulty of distinguishing at this stage of dissection between the M. caninus, M. incisivus superioris and pars peripheralis M. orbicularis oris, is also well illustrated.

The external maxillary artery is seen to pass transversely through the modiolus and deep to the M. caninus and M. incisivus superioris. It emerges again between the latter muscle and the pars peripheralis M. orbicularis oris. The large caput longum M. triangularis is well seen and has already been described. The dotted lines indicate the deep fibres from the medial margin which pass to the M. buccinator and the basis modioli.

43. Modiolus on the right side of the face of No. 2325.

The deep head of the M. zygomaticus is not shown. The aberrant superficial fibres are seen passing to end in the lower end of the naso-buccal gyrus.

Platysma: notice the well-developed nape platysma as well as a well-developed neck platysma showing both a pars aberrans and a pars labialis. The M. triangularis shows all four capita well represented, viz. capita longum, transversum, latum and buccale. Notice the fibres of the M. incisivus inferioris and pars peripheralis M. orbicularis oris inferioris ending in the skin (dotted area).

Table C (*continued*)

44. Of the muscles of the left side of the face of No. 2325.

Pars peripheralis M. orbicularis oculi: notice the large well-developed caput laterale. This is shown cut across. It ended in the gyrus naso-buccalis. The caput mediale shows the ill-developed medial fibres lying superficial to the caput angulare. The lateral fibres of this head are better developed and lie superficial to the caput laterale.

M. quadratus labii superioris: here again the fibres of the caput angulare which end in the naso-labial fold hides from view the labial fibres of this head until they are seen in the lip area.

Caput zygomaticum is again divided into a superficial and a deep portion, the deep joining the M. quadratus labii superioris and the superficial ending in the naso-buccal gyrus.

M. zygomaticus: the deep portion is not seen. Notice on this side also the aberrant superficial medial fibres ending in the lower end of the naso-buccal gyrus.

Platysma: shows both nape and neck platysmae and the latter shows a pars aberrans and a pars labialis.

M. triangularis shows again four well-developed heads—the capita longum, transversum, latum and buccale. Notice the abnormal position of the caput buccale and some of the shortest and most lateral fibres of the caput latum. Inferior to the caput buccale is a long narrow ribbon-like muscle band stretching from the parotid region to beneath the chin. It lies superficial to the fibres of the platysma but beneath the fibres of the caput latum. This is probably a remnant of the inferior auriculo-labialis muscle or M. mandibulo-marginalis. It was not present on the right side.

45. Of the muscles of the right side of the face of an eight months foetus of European origin. This was enlarged one and a half times.

Pars peripheralis M. orbicularis oculi was well developed. The caput laterale covered completely the other muscles in this region and its fibres proceeded across to end in the gyrus naso-buccalis and upper lip. They are here shown in part only so as to view the underlying muscles.

Caput mediale was also well-developed. It crossed superficial to the caput laterale and ended in the lateral portion of the gyrus naso-buccalis. It likewise covered to a large extent the other muscles in this region. No medial portion of this caput was seen and so the caput angulare M. quadratus labii superioris was seen for a large part of its course.

M. quadratus labii superioris: the caput angulare was well developed and the nasal and naso-labial fibres were easily distinguished. The labial fibres were not easy to demonstrate in this small subject. Caput infraorbitale was seen to pass posterior to the naso-labial fibres of the caput angulare.

Caput zygomaticum and M. zygomaticus: this caput, together with the M. zygomaticus formed a large sheet of muscle running almost parallel with the caput laterale of the pars peripheralis M. orbicularis oculi though on a deeper plane. It was formed only by the superficial fibres of these two muscles and ended in the gyrus naso-buccalis. The superior fibres passed deep to the naso-labial fibres of the caput angulare M. quadratus labii superioris. The deeper portions of the caput zygomaticum and the M. zygomaticus are not visible.

The lateral superficial fibres of the M. zygomaticus ended partly in the modiolus and a few curled posteriorly to join the caput buccale and a few others ended in the panniculus adiposus of the cheek superficial and anterior to the corpus adiposum buccae.

M. triangularis: this muscle was relatively more extensive, thicker and more powerful than those dissected in the adult not even excluding the two Australian aboriginals. It is true that the heads of the European were from elderly subjects but the aboriginals were both middle aged males. The muscle stood out from the underlying platysma in bold relief as a very large and unbroken fan of curving muscular fibres.

Caput buccale: this was formed by the superior fibres of this mass and was easily to be distinguished as the fibres ran almost transversely laterally and did not tend to curl inferiorly. In none of the subjects dissected did the fibres of the caput buccale show any tendency to curl inferiorly.

Caput longum: this was completely hidden from view by the capita latum and transversum. Caput transversum was a well-developed muscular sling extending from modiolus to modiolus and lying superficial to the platysma.

Caput latum: this was very well developed and possessed an unusual number of powerful curved muscle fibres medial to the caput longum.

The apex modioli was 0·5 cm. away from the angle of the mouth and the most superficial fibres

Table C (*continued*)

at the apex modioli came from the superficial portion of the pars peripheralis M. orbicularis oris and not from the M. zygomaticus.

Platysma: this showed both a pars aberrans and a pars labialis. Both the M. buccinator and pars transversa M. nasalis are seen in the tracing.

Note that in the dissection of the foetus the muscularity of the face is infinitely greater and more primitive than that of the adult; that is to say, not only are the muscles relatively much greater in size, but they have a much wider distribution and resemble rather the aboriginal than the European face.

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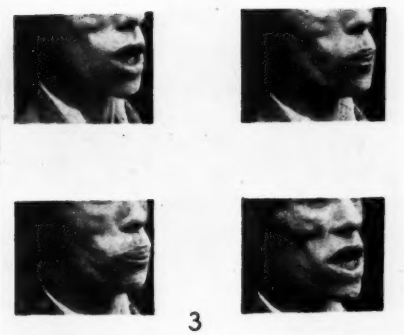

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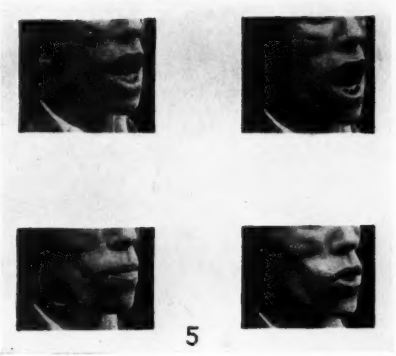
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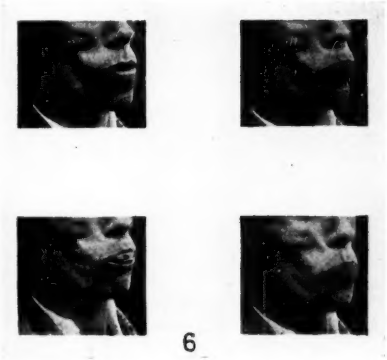
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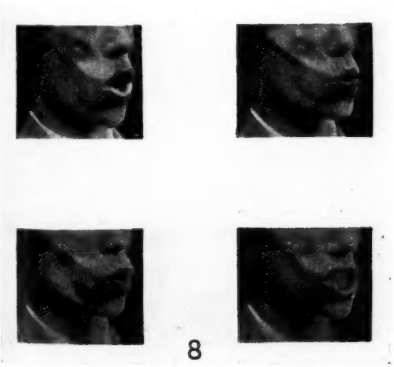
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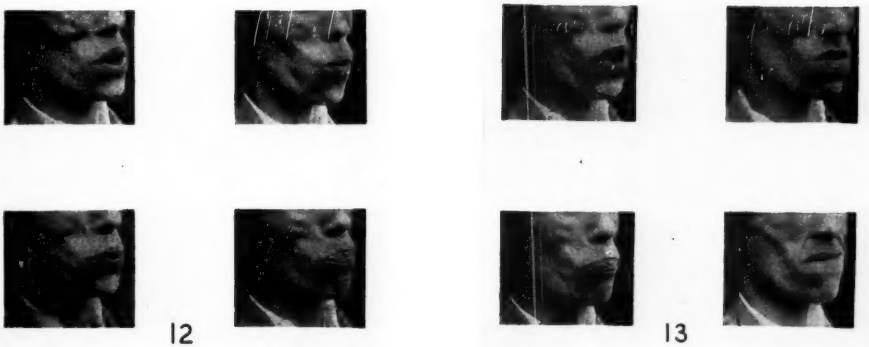

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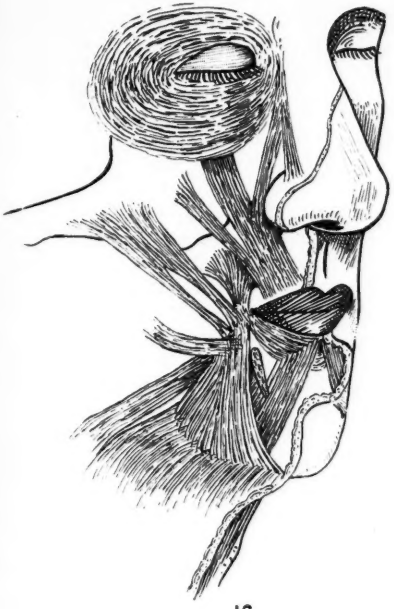

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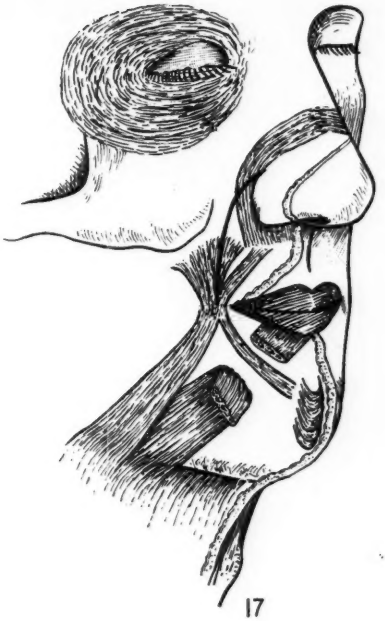

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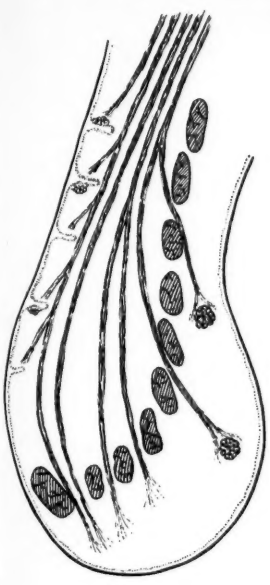

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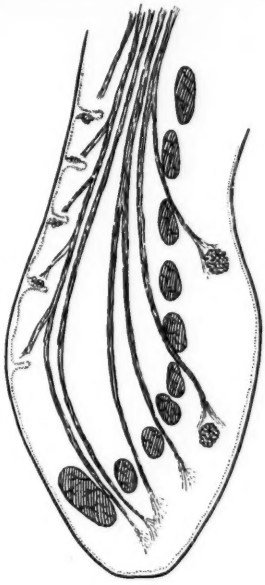

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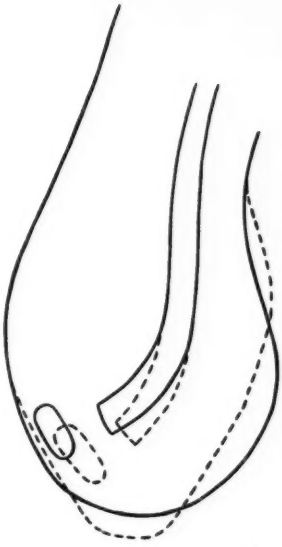

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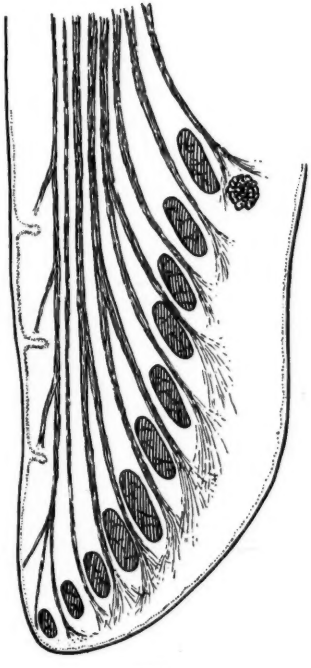

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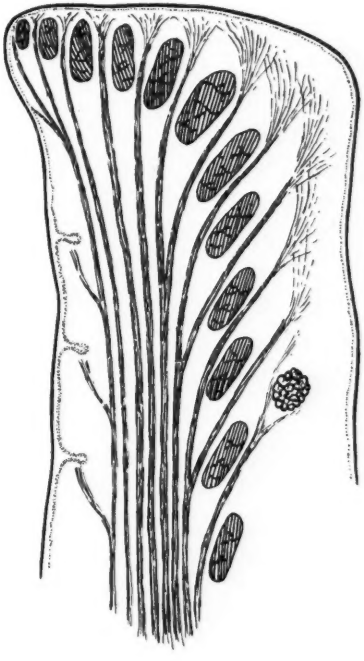

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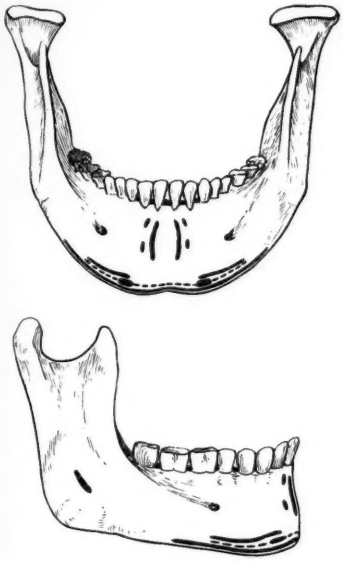

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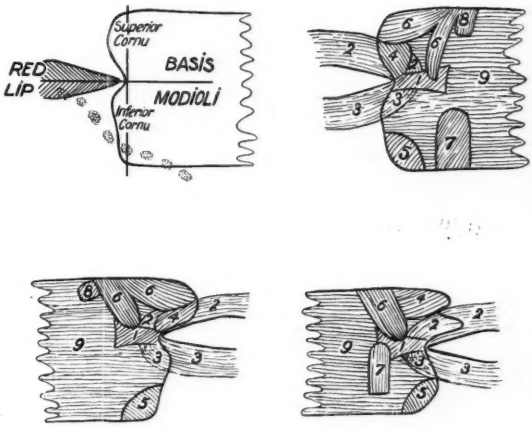

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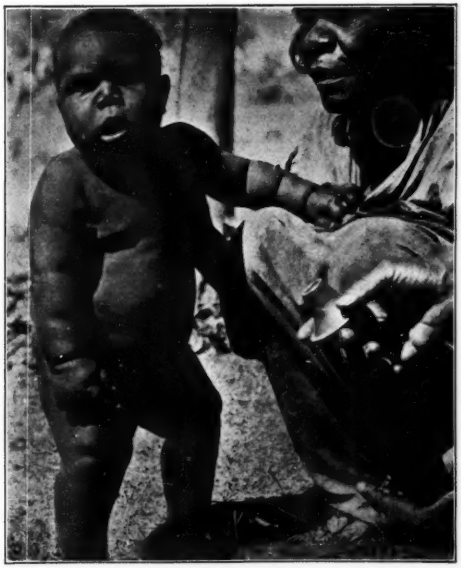

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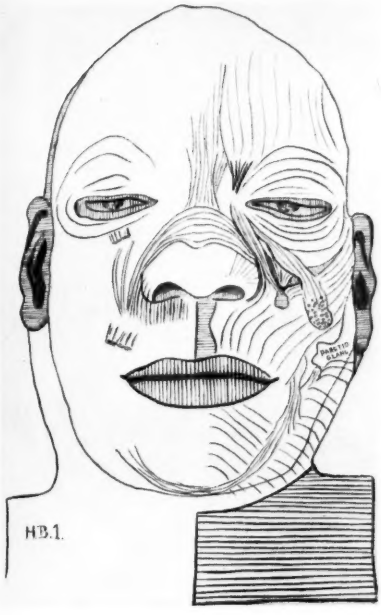

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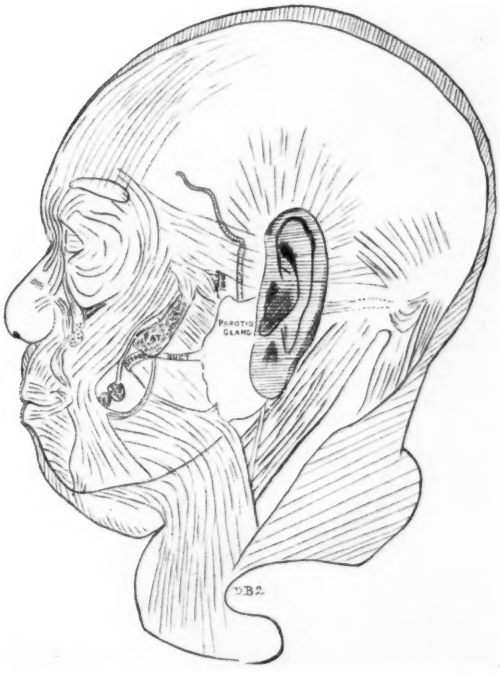

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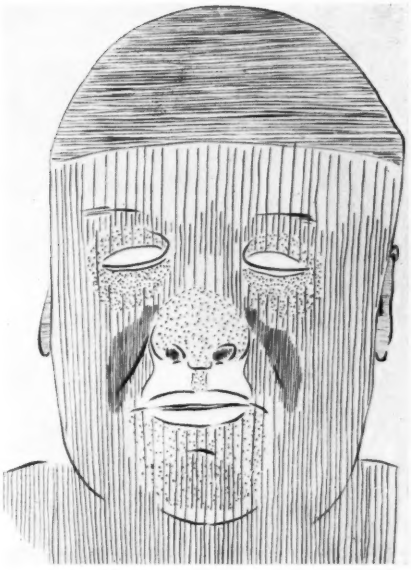

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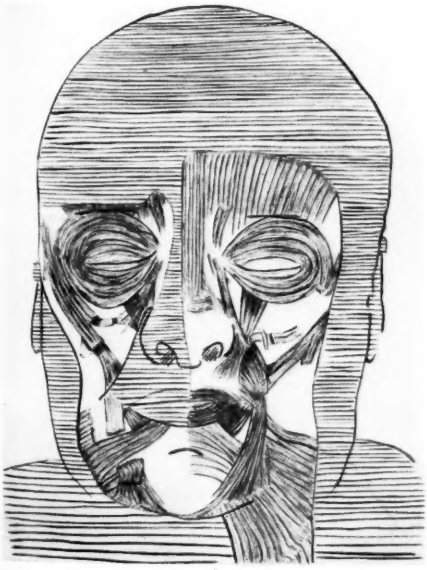

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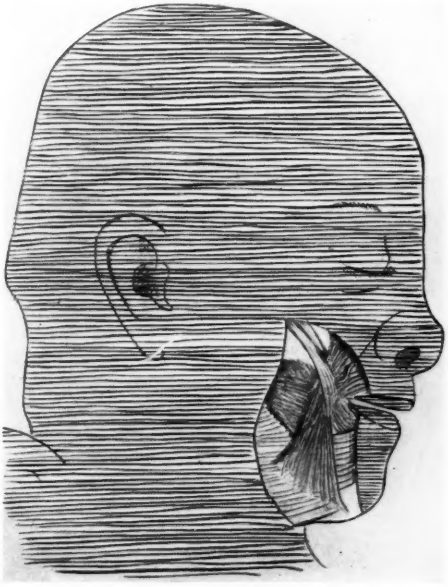

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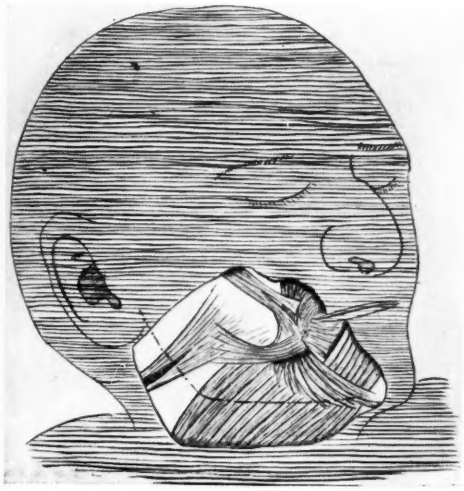

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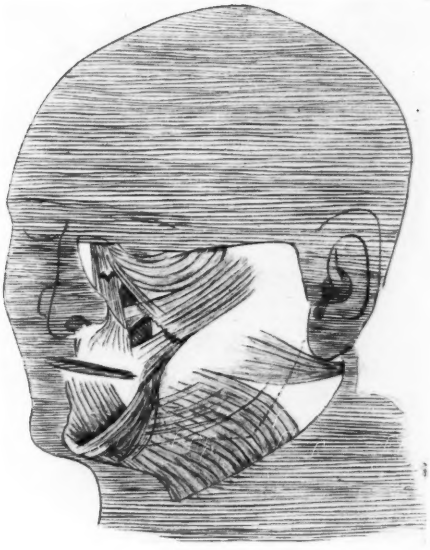

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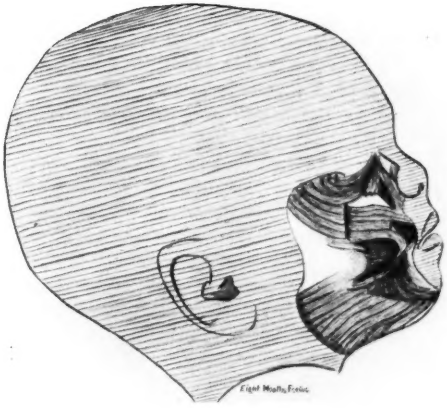

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THE CORTICAL LAMINATION OF *TARSIUS*

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The zoological affinities of *Tarsius* give to its anatomy and particularly to the minute anatomy of the central nervous system a very great interest. The evidence seems to suggest that it is closely related to the menotyphlous Insectivores and the primitive ancestors of the mammalian stock. It is moreover a member of the family Lemuroidea and stands close to the base of the Primate stem.

It is merely platitudinous to assert that the key to the evolution of the Primate stock lies in unravelling the factors that have led to the great increase in the extent of the cerebral cortex. Amongst these factors vision must play a primary role. In addition to its mental significance, Magnus has shown that in Primates and in Carnivores, vision plays a fundamental part in postural reflexes and in the maintenance of muscle tone.

Professor Elliot Smith has pointed out (1912) the peculiar significance of *Tarsius* in understanding the evolution of the Primates; it has a marked increase in the retinal areas, but above all the necessary spatial increase in the cortical areas for vision and visuo-psychic functions. The importance of this is appreciated when we recall that the various events in the evolution of vision are spatially represented in the cortex and that, for instance, stereoscopic vision seems to need a special cortical centre. The loss of the appreciation of the position of an object in space and also a loss of the sense of solidity may follow from an occipital injury though out-line and the other characteristics of visual perception are retained. (Riddoch.)

The eyes of *Tarsius* are grotesquely large. The natives regard its twilight appearances with awe and fear. The retina is of the nocturnal type and on the lateral side of the entrance of the optic nerve there is a differentiated area in which the percipient elements and the ganglion cells are increased. The ocular muscles are inserted around the posterior pole of the eye far away from the corneo-sclerotic margin. It has been observed that it moves its head and not its eyes. This is further corroborated by the excellent development of suboccipital muscles and the close approximation of the occipital condyles. The optic nerve to enter its foramen turns almost directly inwards at first and after passing through the foramen the two nerves run parallel to the chiasma; here, however, complete decussation of the two nerves takes place. The pulvinar and the lateral geniculate bodies are indeed very large. It is evident from these facts that the change in the peripheral mechanism of vision consists in two things—reduction of the face so permitting binocular vision and secondly great increase in the retinal areas.

The material for this study was kindly given us by Dr Charles Hose and Mr Le Gros Clark. The brains had been preserved in 10 per cent. formalin. They were cut into frontal and horizontal series of sections of 10μ and stained with toluidin blue. Toluidin blue works well after formalin and is relatively permanent if the sections are treated after staining with weak sodium carbonate. All the formalin should be got rid of and the stay in the alcohols should be prolonged.

The brain is a smooth one, but there is of course a hippocampal fissure, a deep and well-developed calcarine fissure, a rudimentary sylvian fissure, but no rhinal fissure. The great size of the eyes has excavated deeply the frontal lobes. These are of very small size. The temporal pole is large but the mesial surface is deeply excavated by the great size of the mesencephalon. The mesial surface of the occipital area is in its lower part deeply concave but above this concavity an elevation of the mesial surface overhangs the depression. The olfactory bulb is small and extends about 3·5 mm. beyond the frontal pole. The secondary olfactory centres are inconspicuous. The tertiary areas hippocampus and fascia dentata are substantial. The corpus callosum is small, the ventral commissure considerable. The average length of the brain is about 14 mm. Seen from above it is widely expanded transversely.

In studying the cortical stratification one must perforce follow the admirable researches of Brodmann. This observer has covered in his papers examples of most mammals of phylogenetic value and particularly the Primates. Throughout he has used a consistent nomenclature, and adopted the same criteria, for the identification of particular areas. As others have found it is difficult to reach precise agreement as to the characters and more particularly the extent of certain areas since these depend on minutiae whose recognition and interpretation must vary with the individual. There is no doubt however that the minute and wide investigations of Brodmann, his nomenclature of the six layered cortex (originally used by Bevan Lewis), and his denominations of the areas make it essential to follow him for purposes of comparison. Brodmann has published descriptions and figures of the cortex of *Lemur* and *Nycticebus*. *Lemur* was also studied by Mott and Kelly but not in the same exhaustive and minute fashion. *Tarsius* was investigated by Elliot Smith. The figures which he gives appear in Duckworth's *Text Book of Comparative Anatomy*. They were arrived at by the same method that was used in his study of the cortical areas of the human brain. We are in substantial agreement with his map of the cortex of the brain of *Tarsius*.

In general it may be said that *Tarsius* shows a great area striata and surrounding this a wide area occipitalis (18 and 19), i.e. the visuo-psychic area of Campbell. The motor area is far forward and the frontal is compressed, small and little differentiated. The temporal and parietal areas are less differentiated than the corresponding areas in *Lemur*. The cingular area except in its posterior part is composed almost entirely of one type. The presubicular region which in *Lemur* seems divisible into several types is comparatively

uniform in *Tarsius*. On the whole the brain of *Tarsius* shows a reduction in the secondary olfactory centres; it shows a segregation of its cortex into the main cortical subdivisions but without proceeding far in the further specialisation of these main areas except in regard to vision where there has been a great increase in extent both of the area striata and the adjacent para-striata area. Its generalised state and the trend of its changes are such that it serves as the starting-point for the subsequent expansion that continues right up to man.

THE DESCRIPTION OF THE INDIVIDUAL AREAS

We reproduce the cortical maps of the lateral and mesial surfaces of the brain. We begin with area 1—the area post centralis.

This area is a narrow zone which is separated from the motor cortex lying in front by nothing more definite than a slight widening of the lamina zonalis. There is thus no indication of a central sulcus. In other parts of the brain morphological boundaries are apparent as slight infoldings of the lamina zonalis. These are very slight but quite precise and definite in position. The posterior boundary is definitely marked by one of these foldings of the outer zone thus affording to this area a morphological limit posteriorly. On the mesial surface of the brain there is another slight infolding of the outer zone separating it from the cingular area. In the lower part of its lateral area it is very much narrowed as it approaches the insula.

The particular characteristics of the cell laminae are as follows:

The lamina zonalis. This presents no features of note. As it approaches the motor area it gradually increases in width.

The lamina granularis externa. This is rather more definite than is usual in this brain. On the whole this lamina is very indefinite in *Tarsius*. However in this region it is identifiable as a layer of cells three or four thick and of the granular type.

The lamina pyramidalis. This layer is only imperfectly separated from the lamina granularis externa. In the motor area there is a quite sudden definition of this layer again and similarly in the area 5 and 7 posteriorly it is well defined. At first one would gain the idea that this layer had suddenly broadened but closer inspection shows that this is not the case. The change is really due to a gradual fusion with the internal granular stratum. The confusion between these two layers is further added to by the cells of this layer. They have become much smaller in size and scarcely exceed those composing the granular layer. There is no demarcation into an inner and outer layer.

The lamina granularis interna. This layer is particularly badly defined from the lamina pyramidalis and towards the lamina ganglionaris it is not well defined for here it becomes mixed with slightly larger cells scattered about amongst the smaller granular cells. To the outer side the cells are closely packed but in the inner portion the cells are more diffusely arranged. The lamina as a whole is much broader than the corresponding layer in the area 5

and 7 while in the motor zone the internal granular is reduced to negligible proportions.

The lamina ganglionaris. This is badly defined from the granular layer on the outside but is marked off from the sixth layer by a comparatively acellular zone. The cells composing this lamina in its outer portion are of medium size. In the deeper portion they are larger and are irregularly scattered. These larger cells are most numerous in the middle of the area and are not so numerous towards the anterior and posterior margins.

The lamina multiformis. This layer is separated from the medullary portion of the brain somewhat imperfectly. The cells are not closely packed, are of moderate size and fairly uniform. The layer as a whole is broad and diffuse. Brodmann has established in higher brains a subdivision of this area and suggests that it is possible to distinguish such an arrangement in the cortex of *Lemur* though much more difficult. He states that the differences are only slight. The area in *Tarsius* is quite uniform save for the break that occurs in the lamina ganglionaris just before it joins the motor area in front and the area 5 and 7 behind.

The area as a whole is broad. In man and the higher apes it is strikingly narrow. It is characterised throughout by an abundance of small and medium sized cells. This character makes the lamina granularis interna broad and diffuse and difficult to separate from the adjacent layers and reduces the size of the lamina pyramidalis which layer is noteworthy throughout for the smallness of its cells.

Area 4. The Motor Area.

This occupies the same relative position as in the other Prosimiae. When traced towards the mesial surface of the hemisphere there occurs a slight indentation on the surface of the brain and subjacent to this the lamina broadens out and dips into the outer layer of cells. This is a clear indication of the beginning of morphological boundary and separates the area of giant pyramidal cells from the area cingularis.

The indentations occurring on the brain of *Tarsius* are of two types. There are the indentations arising on the surface often but not always associated with a blood vessel. This is a simple biting of the outer surface without any deformation of the subjacent layers of cells. A second type occurs when such an indentation no larger than the preceding form leads to a depression and a deformation of the subjacent layers. Thus in these so-called smooth brains fissures do begin as the microscopic indentations and the sort of fissure thus beginning is of morphological and physiological significance.

On the lateral surface of the brain such an infolding of the lamina zonalis with a surface indentation begins where the motor area passes over to the insula. On the mesial surface a similar slight displacement of the outer zone indicates a limitation of the motor area from the area cingularis. There is however no indication of boundary either in front from the area frontalis, or

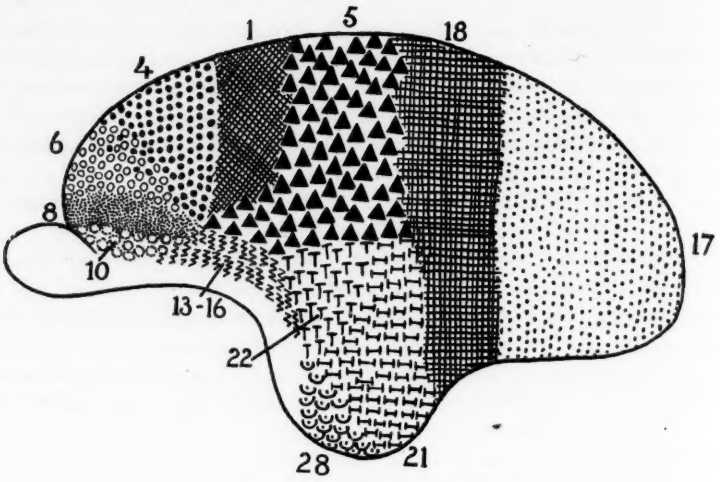

Fig. 1. Lateral view of Cerebrum of Tarsius.

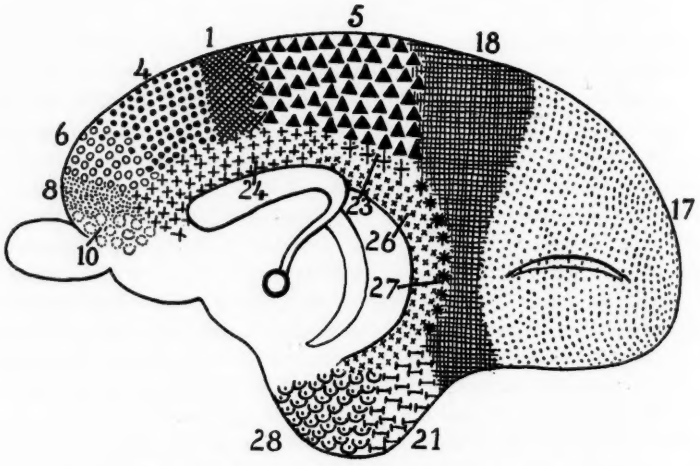

Fig. 2. Mesial view of Cerebral Hemisphere, Tarsius.

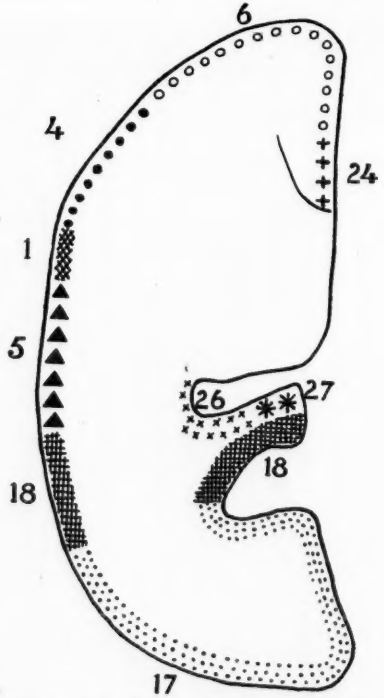

Fig. 3. Dispositions of areas in Horizontal Section. Near the Dorsal Surface of the Hemisphere.

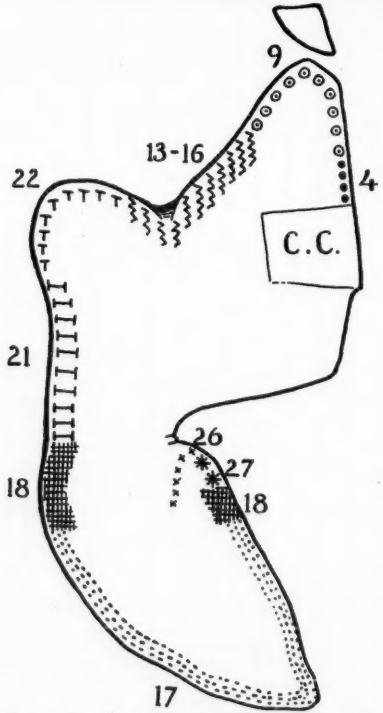

Fig. 4. Horizontal Section near middle of the brain.

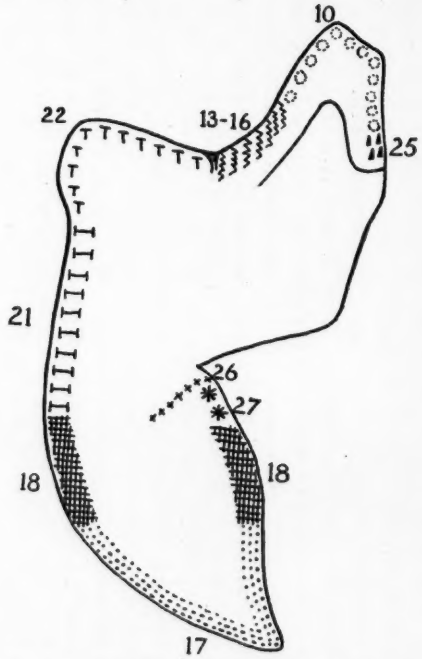

Fig. 5. Horizontal Section near Ventral Surface of the brain.

posteriorly from the area post centralis. In common with the Lemurs and the Anthropoids the width of the motor cortex is very great and is only exceeded by that of the upper part of the insula. The size of the Betz cells is not a very conspicuous feature in *Tarsius*. Many factors have been suggested as influencing the size of cells such as the wealth of associations and the coarseness or the fineness of the movements. In general it would seem that the most important factor is the length of the axis cylinder. The size of the Betz cells in *Tarsius* probably is related to the very small size of the animal. Brodmann has however collected some examples of small animals which have large Betz cells, e.g. in small Carnivores they seem to be as large as in the larger Carnivores. Other general features of this portion of the cortex besides the great width are the lack of definition between the lamina multiformis and the white matter of the brain, and the loose packing of the cells; further the whole area is characterised by a larger type of cell throughout, while the smaller granular cell is so infrequent that the layer of internal granules is almost wanting. Above all the presence of the Betz cells render the identification of this area easy.

The features of the individual layers are as follows. The lamina zonalis is broad and is succeeded by a lamina of cells in which it is impossible to identify a lamina granularis externa. The lamina pyramidalis is very narrow and composed of larger cells than elsewhere. In man this layer is extremely broad. In *Lemur* Brodmann records that this layer is extremely narrow and so it is also in *Tarsius*. All observers agree in recording the absence of the lamina granularis interna from the motor area. However in a recent study of the cortex of the American Opossum by Gray, it is said to be present. In *Tarsius* there is an indefinite stratum very narrow and irregular which represents this lamina.

The cells are of the usual granular type. They however can hardly be said to constitute a definite layer and *Tarsius* therefore resembles the Primates rather than the more primitive forms.

The lamina ganglionaris contains the Betz cells. These are arranged in rows several cells thick which in general run to the surface of the cortex. However here and there they tend to form clusters, of three or four cells. Between the large Betz cells the cortex is astonishingly free from cells only a few scattered elements are visible here and there.

The lamina multiformis is extremely broad and more closely packed with cells than any of the other layers. The individual cells are here larger and there is no sharp definition from the underlying white matter. As a whole the motor cortex is thrust far forward and the frontal is reduced to relatively small proportions. The lamina ganglionaris compared with other areas is much closer to the surface.

A detailed comparison with the same area of *Lemur* is as follows:

Lemur (Brodmann)	*Tarsius*
(*a*) Great width of the cortex as compared with the post central area.	Same feature present.
(*b*) Cortical breadth is one-third less than in man but the same as in the Apes.	Not so wide as in *Lemur*.

Lemur (Brodmann)	*Tarsius*
(*c*) Gradual transformation of lamina into subjacent white matter.	Same feature.
(*d*) Cell density less than in higher types.	The cell density less than in *Lemur*.
(*e*) Large cell forms dominant and granular elements reduced.	Cells not so large and the granular elements not so reduced.
(*f*) Stratification rather imperfect. Internal granular layer is wanting. Betz cells arranged parallel to the surface.	Stratification is also imperfect but the reduction of the internal granular layer is not so complete. The arrangement of the Betz cells is similar.

The Area Parietalis and Preparietalis. Type 5 *and* 7.

This area lies between the area occipitalis behind, from which it is separated by a widening of the cortex, and an infolding which is marked by a sudden increase in the width of the lamina zonalis. This slight dip persists only for the briefest distance. The pucker on the surface is hardly visible under the microscope. Anteriorly it extends towards area 1, the area post centralis. The area occupied by this (5 and 7) we find to be not so extensive as the area 18 and 19. In the lemuroid and simian brain as figured by Brodmann the cortical surface allotted to 5 and 7 considerably exceeds that of 18 and 19. In the rabbit and *Erinaceus* these areas cannot be accurately defined as the two types of lamination are intermixed. The boundary between the two is sharp in *Tarsius* and can be easily appreciated. The size of the area 18 and 19 can no doubt be correlated with the size of the area striata. The anterior boundary of this area from area 1 we again find marked by a dimpling in and a slight thickening of the lamina zonalis. This indenture is again only visible on the surface in the slightest degree. Mesially it is separated from the area 25 by a slight indentation and thickening of the lamina zonalis. Laterally it approaches the area 22.

In *Lemur* Brodmann has subdivided this area into two portions 5 and 7 by the cell characters of the lamina pyramidalis and lamina ganglionaris. In *Tarsius* the arrangement seems quite different. As one passes from the visual area forwards through the area 18 and 19 the only change one notices is a very slight increase in the depth of the cortex. The cell sheeting and the individuality of each layer remains unchanged. The whole of this area is characterised by the decision of the lamina granularis interna.

When the area 5 and 7 (parietalis of Brodmann) is approached there is a transition to a new type which is characterised by a less definite lamina granularis interna and an increase in the size and number of the cells in the lamina ganglionaris. Therefore we think that the subdivisions of the areas occipitalis (18 and 19) and parietalis (5 and 7) in *Lemur* have in *Tarsius* remained undifferentiated.

The characters of each cell lamina in area 5 may be put down as follows:

The lamina zonalis is somewhat narrower than usual.

The lamina granularis externa is better marked here than in most other areas.

The lamina pyramidalis. This is considerably broader than in area occi-

pitalis 18 and 19, in fact almost double. An outer and inner portion can be distinguished by the size of the cells. Those occupying the inner portion are much larger than those in the outer and it is due to these that the increase in width has taken place. These cells press down amongst those of the next layer.

The lamina granularis interna is much narrower and is not so sharply defined. Not only is the total width reduced but also the cells are not so closely packed.

The lamina ganglionaris contains many medium and large cells and has a slight resemblance to the motor cortex but the cells are not so large and they have none of the regular arrangement found among the Betz cells of the motor cortex. They are closely packed against the lamina granularis interna, and an area comparatively free from cells separates this layer from the sixth layer. In the motor cortex the Betz cells tend to extend into the lamina multiformis.

The lamina multiformis appears diffuse owing to the broadening of the lamina ganglionaris. It contains more large cells than the same layer in the area 18 and 19. It is however sharply marked off from the underlying white matter.

Area 6. *Area Frontalis Agranularis.*

This area and the area labelled 8 and 9 are all very much alike. The only difference that can be perceived is that area 6 is somewhat broader and more richly cellular. It passes behind into the motor area to which it presents considerable similarity. The differences between this frontal area and the motor area are definite. The differences are the greater width of the lamina pyramidalis, the size of the cells of the lamina ganglionaris which are smaller than the cells of the corresponding layer of the motor area, are more deeply situated in the cortex and have a regular arrangement in vertical columns, palisades. It however resembles the motor area in the great reduction of the lamina granularis interna, in the presence of numbers of large cells, in the great width of the cortex, in the thickness of the lamina multiformis, and its transition into the medullary substance, without any sharp line of demarcation.

The particular features of the cell laminae are as follows:

The lamina granularis externa consists of a few scattered cells and as in most other areas in *Tarsius* is very indefinite.

The lamina pyramidalis is broad and can be divided into an outer zone and an inner zone. The outer zone which occupies about two-thirds of the stratum consists of moderate sized cells which stain more deeply than the inner portion. The inner portion consists of slightly smaller cells which stain less intensively. The deepest of this layer contains the smallest cells and resembles those associated with the lamina granularis interna. There is however no accumulation of these cells into a definite stratum and the lamina granularis can hardly therefore be said to exist.

The lamina ganglionaris is very well marked and consists of large cells

which resemble but are smaller than the Betz cells. The cells press up against the lamina pyramidalis and are arranged regularly in vertical rows. Each vertical row consists of about six or more of these large cells. A more or less acellular area separates this layer from the lamina multiformis, thus differing from the motor area where the giant cells press down into the sixth layer.

The lamina multiformis is broad and closely packed with middle sized cells. These are regularly arranged and of a pretty uniform size. This layer is separated by an acellular layer from the lamina ganglionaris. It is ill defined as it approaches the white matter of the brain.

Area 8. *Area Frontalis Granularis.*

This area in *Tarsius* corresponds with the areas 8 and 9 that Brodmann separates in *Lemur*. The separation depends on differences of cellular arrangement in the lamina ganglionaris. This in area 9 in *Lemur* is divisible into an inner and an outer layer. In *Tarsius* this area does not permit of any such subdivision. It is a very broad area in cortical width and distinctly well stratified, while the characters of the cell layers are uniform. The area as a whole is small and is pressed down towards the base of the frontal pole. The lamina granularis interna is only very poorly marked. In *Lemur* the possession of a well-marked internal granular is one of the principal points of separation from the area 6.

The various layers may be described as follows:

The lamina zonalis is broad.

The lamina granularis externa does not exist.

The lamina zonalis is immediately succeeded by fairly large cells somewhat irregularly arranged belonging to the lamina pyramidalis.

The lamina pyramidalis seems to be composed of two layers, an outer portion of large cells which stain deeply, and an inner portion composed also of large cells yet somewhat smaller than the outer ones. They stain much less deeply. Here and there are a few small cells, but arranged in no regular fashion and a true lamina granularis does not exist.

The lamina ganglionaris is close up against the deep surface of the lamina pyramidalis. The cells are fairly large and more definitely arranged and closer together in the outer portion. On the inner side they are fewer in number, more irregularly arranged, and thus a more or less irregularly acellular area tends to separate the lamina ganglionaris from the lamina multiformis.

The lamina multiformis is narrow, the cells are of medium size and closely packed together. They are sharply marked off from the medullary matter of the brain.

The Area Orbitalis. Areas 10 *and* 11.

This area is the basal portion of the frontal lobe. In the Primates can be separated into an inner and an outer layer. In the *Lemur* Brodmann was unable to find any such difference and in *Tarsius* there is no such distinction to be observed. This area represents a rudimentary piece of cortex in which

all the layers are of small size except the lamina zonalis and in which the granular layers are altogether wanting.

The lamina zonalis is broad and merges with this very broad layer of the insular cortex.

The lamina pyramidalis is very narrow. It is comparatively acellular, the cells being widely scattered. The outer portion is more compact, and for about four or five cells deep is fairly definite. Then it becomes more scattered and small granular cells become interspersed amongst it.

No lamina granularis interna is present as a separate layer. Although granular cells are interspersed amongst the deeper irregular part of the lamina pyramidalis they are arranged is such an irregular fashion that they do not form any regular stratum.

The lamina ganglionaris is diffuse and irregular. It is comparatively poor in cells and cannot be marked with precision from the other layers.

The lamina multiformis is better defined and more compact. It is sharply marked off from the underlying white matter but again its outer portion fuses with the lamina pyramidalis. It is composed of medium and small sized cells.

As a whole the characters of this area are:

Absence of the internal and external granular layers.

The indefinite stratification of all the layers.

The great narrowing of the width of the cortex.

It resembles *Lemur* in that it cannot be divided into an inner and outer area.

The Area Insularis. Areas 13 *and* 16.

The boundaries of this area are nowhere sharply defined except at its lower posterior margin where it meets the sylvian fissure. From above one passes from the parietal area 5 and 7 which comes forwards right to the frontal area intervening between the motor area and the area post centralis above and the insula area below.

Along this upper margin of the insula the cell characters of its cortex resembles those of the area parietalis. It is the portion which Brodmann calls the area insularis granularis. The two principal characters of the insular cortex are just beginning to appear, viz. the great width of the lamina zonalis and the separation of the lamina multiforme into two layers the deeper of which is the claustrum.

In the area granularis the lamina zonalis has increased in the width but has not yet reached its maximum size. The lamina granularis externa and the lamina pyramidalis have fused together into a layer of small closely packed cells. The lamina granularis interna appears to be comparatively acellular. It contains however a number of very small granular cells. It is marked off from the pyramidalis quite indefinitely but from the lamina ganglionaris it is well defined.

The lamina ganglionaris is poorly developed. It consists of a few scattered cells of middle size and some small cells fusing with the lamina multiformis.

The lamina multiformis shows a division into two layers. At the oral and caudal boundaries this layer fuses with the claustrum. The outer portion of the lamina multiformis consists of closely packed small cells and is succeeded by a clear area (the capsula extrema) and then by the inner layer (the claustrum). The cells of this inner layer are larger and not so closely packed as in the outer.

As areas of the insula towards the base are examined, the character of the cortex changes. The lamina zonalis becomes extremely broad and is now twice the width that it is in any other part of the cortex. The outer margin of the cells has become irregular and clumps of cells project into the zonal layer. These are joined to the rest of the cortex only by their borders. The lamina pyramidalis is very narrow. Its cells are of small size and closely packed together. It is succeeded by a broad zone which is strikingly poor in cells. The few cells present either in shape, size, or arrangement, have no definite characteristics, and cannot be labelled either granular or ganglionic. Topographically this acellular layer must represent both the fourth and fifth laminae for it is immediately succeeded by a well-defined lamina multiformis.

This sixth lamina shows the characteristic division into two layers. In its outer portion the cells are large and very compactly arranged while in the inner zone they are much smaller. The cells of the outer layer are arranged vertically to the surface while the inner ones assume a position parallel to the surface. The capsula extrema intervenes between the outer and the inner portion or claustrum. The posterior boundary of the insula in its lower two-thirds is formed by a short and shallow sylvian fissure. In its inferior portion the insula shows still more exaggerated the characteristics described in its middle portion. The lamina zonalis is extremely broad but the cellular zones have become extremely narrow. There is great difficulty in disentangling any layers superficial to the sixth. This outer cellular layer shows on the surface an irregular contour of small cells which have become at points separated from the general mass. It is probably a distinct and well defined external granular lamina. The lamina pyramidalis is very narrow, the cells are very small, and the whole stratum seems to have taken on the characters of a granular layer. Then comes a clear zone in which the cells are so indefinitely arranged and so few, that though it must comprise both the internal granular and the ganglionic layers, these cannot be separated. The lamina multiformis is now again a single layer. The line of fusion with the claustrum is visible in part but elsewhere is complete. The sylvian fissure forms an abrupt boundary to this area posteriorly. The line of transition to the frontal area in front is gradual, and this also applies to the union with the parietal area above, and the temporal area behind. The last portions of the insula immediately above the tuberculum olfactorium have become reduced in size until the whole cortex is only a few cells thick.

Area Striata. Area 17.

The extent of this area is relatively enormous, and with the adjacent area 18 and 19, comprises about one-third of the brain. It is further distinguished

by a well-marked calcarine fissure on the medial surface which probably corresponds to the anterior portion of that fissure in other animals. The interior of the occipital lobe is penetrated by a narrow diverticulum of the lateral ventricle. There is thus a posterior horn which is absent in the *Lemurs*. The characters of the layers are striking and obvious, and this area could easily be identified by the naked eye. The characters are as follows:

The lamina zonalis is narrow—about one-half the size it reaches in the insular region.

The lamina granularis externa is extremely well defined and consists of several layers of small cells closely packed together.

The lamina pyramidalis is narrow and obviously consists of an outer and an inner portion. The outer portion is composed of closely packed cells of small size and is only imperfectly separated from the external granular layer. It is so granular in appearance that the whole layer might be referred to the external granular lamina. The inner portion of the lamina pyramidalis is comparatively acellular and lies sharply defined between the internal granular layer and the outer portion of the lamina pyramidalis. The cells of this inner portion are slightly larger than those of the outer and are very few in number.

The lamina granularis interna. The outer layer of this succeeds the clear area just mentioned and consists of a broad band about eight to twelve cells thick. This is followed by a clear area the Stria of Gennari. This is an acellular band between the two layers of granules. A few scattered cells are to be found in it. The inner layer of granules though quite imposing is not so regular as the outer portion. The cells composing it occupy a wider area than the outer and are most closely packed along its borders. The central portion tends to be paler and to contain fewer cells.

The lamina ganglionaris is extremely wide and is sharply defined along both margins. The cells in it are few and loosely arranged. The area appears pale though there are many cells in it, but these for the most are of small size. Towards the sixth layer there is an occasional cell of larger size—the solitary cells of Meynert. These solitary cells are extremely few and hard to find.

The lamina multiformis is well defined and moderately broad. The outer portion is very compact and composed of small cells. The inner portion is much more loosely arranged and the cells are larger. This layer is sharply marked off from the white matter the cells here forming a very definite margin.

There are thus the following pale areas present in the visual zone:

1. The lamina zonalis.
2. The inner portion of the lamina pyramidalis.
3. The zone between the two layers of granules.
4. The zone of the lamina ganglionaris.

The area throughout is characterised by the small granule cell. Predominating in every layer they are everywhere arranged in an extraordinary compact fashion in regular rows with pale acellular bands intervening between them.

The Area Occipitalis B. 18 *and* 19.

In *Tarsius* it is not possible to subdivide this area occipitalis. Though Brodmann has separated them in *Lemur* he points out that the only basis for such a separation is the slightly narrower width of the cortex which is reflected in the dimensions of the individual layers.

If this area be followed in a horizontal section forwards from the area striata it will be seen that the point where the two layers of the internal granular lamina fuse together is abrupt. The fusion marks the points where the occipital area begins. Each layer of this is well defined and sharply marked from the succeeding one. It differs from the preceding area 17 in that the cortex is narrower, the lamina granularis is reduced to a single layer, and the lamina pyramidalis is much broader.

The characters of each layer are as follows:

The lamina zonalis is of average width.

The lamina granularis externa as in most other areas is not very well marked.

The lamina pyramidalis is slightly broader than in the area striata. It is well defined from the adjacent layers. The cells are regularly arranged and increase in size towards the inner margin. So regular is the increase in size of the cells that the outer two-thirds may be described as a layer of small pyramids, and the inner third, resting on the lamina granularis interna, as a layer of large pyramids.

The lamina granularis interna is seen in very typical form. It is uniformly granular in appearance and its definition is peculiarly sharp and without confusion with the other layers. It is formed by fusion of the two layers of the internal granular lamina of the area striata.

The lamina ganglionaris is rather poor in cells, interspersed among cells of small or medium size are occasional large solitary cells.

The lamina multiformis is sharply marked off from the subjacent white matter. The portion near the fifth layer appears darker owing to its high cellular content while the deeper portion appears paler owing to the fewness of its cells.

As one advances forwards from this layer the width of the cortex gradually narrows. This would be the only basis for subdividing this area into two subdivisions. On the mesial aspect of the brain the area is somewhat narrower and adjoins those portions of the cortex which are transitional to the hippocampus. On the mesial surface there is a considerable expansion in cortical thickness, and the outer portion particularly takes on a granular appearance. This area no doubt belongs to the area occipitalis, slightly modified by the expansion but having the same features. It was probably this area that was described by Koppen and Hermanides and regarded as belonging to the area striata.

The Temporal Area.

In *Lemur* Brodmann has subdivided this area into a superior, a middle, and an inferior temporal field. To the area temporalis superior he allots a space which is much larger than we find to be the case in *Tarsius*.

It is a small area bounded in front by the fissure of Sylvius from the insula. This fissure of Sylvius is only visible in section. In addition to being a smaller area the superior temporal differs in structure from the *Lemur* being of a much more granular form than Brodmann has described.

The special features of the superior temporal area 22 are as follows (Plate IV):

The lamina zonalis, is of moderate width.

The lamina granularis externa is a little more definite than usual.

The lamina pyramidalis is quite narrow and the cells are small.

The lamina granularis interna is better defined here, broader and more closely packed with cells than the neighbouring area of the temporal cortex.

The lamina ganglionaris is poorly marked and its cells are of small size.

The lamina multiformis is composed of small and moderate sized cells. The layer is imperfectly marked off from the subjacent white matter. The whole of this piece of cortex is very broad, the layers are imperfectly distinguished and the cells are predominantly small and granular. In this better defined receptive auditory area from the audito-psychic area *Tarsius* differs from *Lemur* and therein resembles the higher apes and man.

It has not been possible to distinguish between a middle and an inferior temporal and our area 20 corresponds to the 20 and 21 of *Lemur*.

The transition of this area 20 to the piriformis is quite sudden although no rhinal fissure is present. At the actual point of transition there is however an infolding of the lamina zonalis which represents the rhinal fissure. The transition to the piriformis is marked by a cessation of the lamina granularis interna and a fusion of the lamina ganglionaris with the lamina multiformis. There is no demarcation of the temporal area from the parietal or occipital zones.

The characters of the layers of area 20 are (Plate VI):

The lamina zonalis is broad—broader than in the visual area but of course not so broad as in the insular region.

The lamina granularis externa is of considerable thickness relatively. The inner margin is defined only imperfectly by the pyramidal layer where the cells are more loosely arranged.

The lamina pyramidalis is broad. The outer portion is composed of smaller cells closely packed together. The inner portion is composed of larger cells more loosely arranged.

The lamina granularis interna is well defined but narrow. The dotted small cells produce a typical granular appearance. This granular layer is present throughout this temporal area and therefore nowhere corresponds to the inferior temporal since this in *Lemur* according to Brodmann is agranular.

The lamina ganglionaris is well marked. It is pressed up against the granular layer but is separated from the lamina multiformis by a comparatively acellular band. Many of the cells are quite small and only a few are of medium size.

The lamina multiformis is narrow and well defined at both borders. The cells are crowded and of small size.

Area 24. *Area Limbica.*

The anterior of the limbic area is separated above from the motor area by a microscopic infolding of the outer zone. Below it rests on the corpus callosum with the stria. Lancisi intervening. As in *Lemur* the medial stria is well developed while the lateral stria is quite inconspicuous. A division of this area into laminae can hardly be said to exist. In *Lemur* the layers are also indefinite but not to the same extent as in *Tarsius.* The external granular, the pyramidal, and the internal granular laminae do not exist as independent layers, and together they form only a narrow band of cells. The lamina ganglionaris is not marked off from the other laminae but is recognised by the presence of somewhat larger cells.

The lamina multiformis is separated from the subjacent white matter, but outwardly is fused with the other layers. The majority of the cells are small, but a few larger ones are interspersed.

The posterior portion of the area limbica in its transition from area occipitalis (area 18) shows a small area of cortex in which the granular layer (internal) is present. It however is quite reduced and passes so gradually into the occipital area that a definite boundary cannot be determined for either. Apart from this it can be asserted that the area limbica is of uniform structure throughout. Orally the area passes confusedly into the prefrontal area and the area precommisuralis.

Area 25. *Area Presubicularis.*

This area is very narrow and occupies a portion of the cortex which for the most part is turned away from the surface towards the hippocampus. The point of union with the piriformis is abrupt. It is shown by the transformation of the outer layers of the piriformis into granular elements and by the fusion of the fifth and sixth layers into a single sheet which passes on into the large pyramidal cells of the cornu ammonis.

The features of the area are:

The lamina zonalis narrows considerably.

The lamina granularis externa and the lamina pyramidalis and the lamina granularis interna are fused together into a single layer sharply defined externally of narrow dimensions and composed of small cells closely packed together making the whole extremely granular in appearance.

The lamina ganglionaris is not present as a distinct layer but fuses with the lamina multiformis and together they pass on as a single layer. Their cells are rather small and not nearly so large as those of the cornu ammonis with which they appear to fuse.

Area 27. *Area Piriformis.*

In passing from the inferior temporal area to the piriform area there is no indication on the surface of a fissure rhinalis, but at the point of transition

there is an infolding of the lamina zonalis. The surface of the brain remains smooth and there is no sign of a blood vessel at this point. The piriform cortex has a very typical structure and agrees in every way with that of *Lemur*.

The features are:

The lamina zonalis is broad and is succeeded by a definite layer of cells three or four thick. These cells are not of the granular type but are indeed as large as any of the cells of the pyramidalis.

The lamina pyramidalis can be described as consisting of two layers. The outer is composed of larger cells loosely arranged while the inner consists of smaller cells more closely packed together.

The pyramidal layer is succeeded by a narrow band which is practically acellular. Here and there is an odd cell but there is certainly no lamina granularis interna.

The lamina ganglionaris is well defined from the lamina pyramidalis but becomes continuous with the lamina multiformis.

The lamina multiformis is narrow. The cells are large and sharply bounded on their inner surface. The outer portion consists of larger cells more loosely arranged while the inner portion consists of more compact smaller cells.

Area 30. *Area Retro-limbica Agranularis.*

This is a narrow band of modified cortex between the area presubicularis and the area occipitalis and above that granular portion of the area 18 which we believe corresponds to the area of Koppen and Hermanides. It is just a narrow band very like the piriform area.

The lamina zonalis is narrow.

Both the granularis interna and externa are wanting.

The lamina pyramidalis is a narrow band of medium sized cells. It is followed by a pale acellular stratum.

The lamina ganglionaris is wanting.

The lamina multiformis is a narrow band of moderate sized cells and small cells arranged in a confused manner.

The difference between *Tarsius* and more primitive creatures apart from such matters as the relative size of the brain (the proportions of neopallium and archipallium) is seen in the segregation of the principal areas of the cortex. When *Tarsius* is compared with *Erinaceus* for instance there is, apart from the primary receptive areas, an imperfect separation in the latter of the different types that make up the associative areas of the brain.

In *Tarsius* we can therefore see that enhanced cortical discrimination is accompanied by a fuller sorting out of the cortex into structurally homogeneous areas.

It is apparent, moreover, in some respects that *Tarsius* remains a primitive animal for in addition to the macroscopic features already mentioned the cortex bears traces of more primitive structural arrangements. The primitive

cellular types are the small granular receptive cell and the very much larger efferent cell of pyramidal form. As a later development there is interwoven between these a stratum of medium sized pyramidal cells efferent to adjacent areas of the cortex. This succession of cellular types is confirmed by embryology and comparative anatomy. The greater granularity of the cortex of *Tarsius* is shown not only in the purely receptive areas but also in the motor area, the area parietalis and area 20, corresponding to the middle and inferior temporal area.

The greatest granularity prevails in the visual area, for the whole of this very large area practically exhibits no other type of cell than the granular. The cells of Meynert are certainly not numerous in any of the Primates, yet in *Tarsius* they are almost impossible to find. It is probable that these cells are associated with the power of fixation of an object and their paucity may be correlated with some aspects of the behaviour of these creatures. They are extraordinarily numerous in the carnivores.

Apart from this primitive feature in cellular type, in all other respects *Tarsius* shows its affinity with the Primate stock. This is abundantly apparent in the extent and disposition of the principal cortical areas all of which are present. It exceeds *Lemur* in the reduction of the primary and secondary olfactory centres, in the much slighter differentiation of the retro-limbic area and also judging from Brodmann's description and pictures, in the much more precise localisation of the receptive auditory area. It falls short of *Lemur* in the extent and the differentiation of the associational areas. These areas are larger in *Lemur*. This is very much the case in the frontal area. Furthermore these areas have all been subdivided in *Lemur* by Brodmann. As is stated by him the grounds of this subdivision are very slender. In *Tarsius* we have not been able to find any basis for such a subdivision of these associational areas. In one point we must qualify our statement that in *Lemur* the annexes to the receptive area exceeds those of *Tarsius*. The area 18, the area occipitalis, which immediately adjoins the visual area, is more extensive in *Tarsius* than in *Lemur*, but its periphery cannot be distinguished as a distinct area 19.

In general we might say that *Tarsius* has precisely defined receptive areas characterised by a granular type of lamination more undiluted with other elements than in say *Lemur*. This type is carried to an astonishing degree in the visual area. Adjoining these receptive areas the so-called psychic zones—what we might call the areas of percepts—composed of a mixture of granules and pyramids are present and in the case of the visual area more extensive than in *Lemur*. In keeping with the psychological quality of perceptual processes the type of cellular lamination is mixed. By insensible gradations percepts pass into concepts and so localisation becomes indefinite and along with this runs the indefiniteness of the cellular pattern. Here we find that *Lemur* has achieved slightly more subdivision than is the case in *Tarsius*.

In every way this cortex in all its trends foreshadows the anthropoid brain both in what it does and what it avoids.

Though *Tarsius* is a primitive animal and its brain shows on the whole a very straightforward pattern yet it does not throw much light on the problem of localisation. It has been suggested that the insula is concerned in the reception of taste. It is a uniform area save at its approximation to the parietal and the frontal areas. Its cellular pattern is of the non-granular type cells of pyramidal form and of medium size being the predominating type. In consequence of this one would suggest that its function is to be sought in some form of associational work to some receptive area. Such a receptive area might well be that of taste though of this there is no evidence. The same remarks apply to the limbic area. This area in *Lemur* and others is subdivided but in *Tarsius* it is uniform and again its cellular structure suggests that it stands in some associational relationship with some receptive area. If this should be olfaction it would furnish additional evidence that in *Tarsius* the Primates were beginning to abandon the use of the archipallium except in a minor way.

SUMMARY

1. On a basis of cellular lamination the cortex of *Tarsius* has been subdivided into homogeneous areas, see maps, figs. 1 and 2.

2. A comparison of the cortical pattern has been made with other types, particularly *Lemurs*.

3. The beginning of sulci as morphological and physiological boundaries has been observed as microscopic indentations and thickenings of the outer zonal band.

Illustrations to this paper were defrayed by a grant from the Royal Society.

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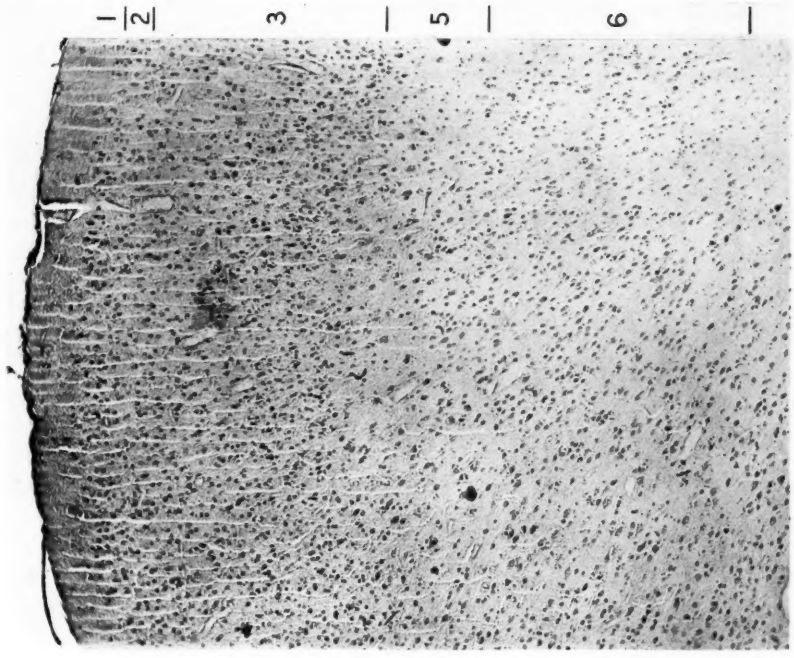

Fig. 2 (Area 4). Motor Area.

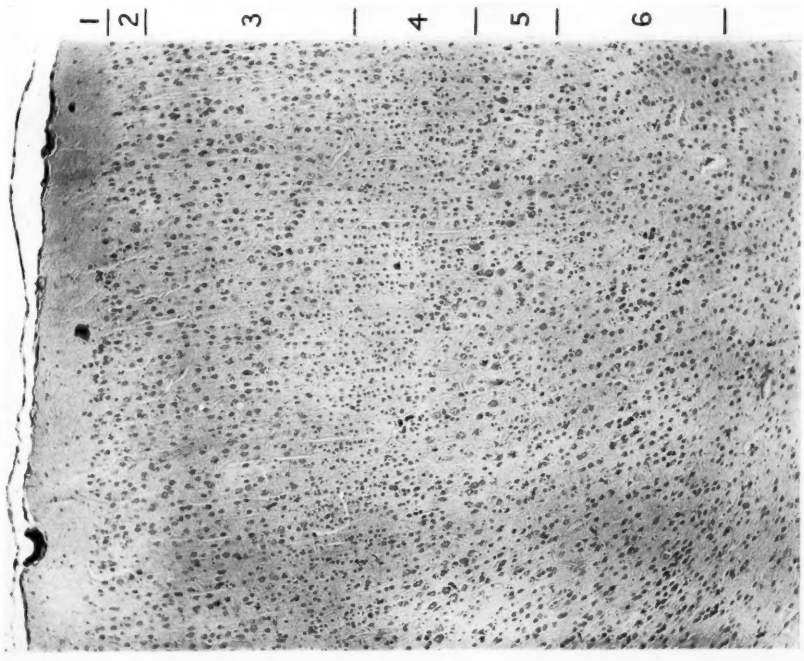

Fig. 1 (Area 1). Area Post-Centralis

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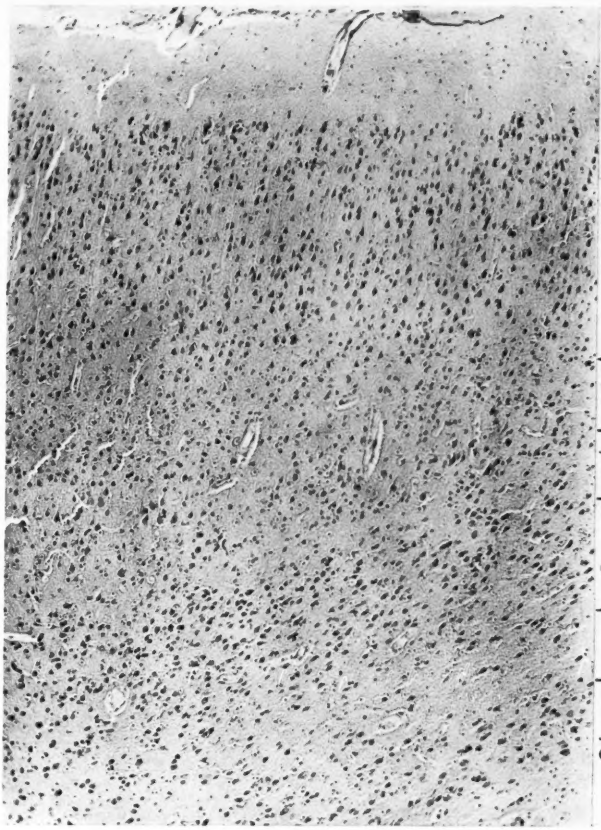

Fig. 4. Area Insularis

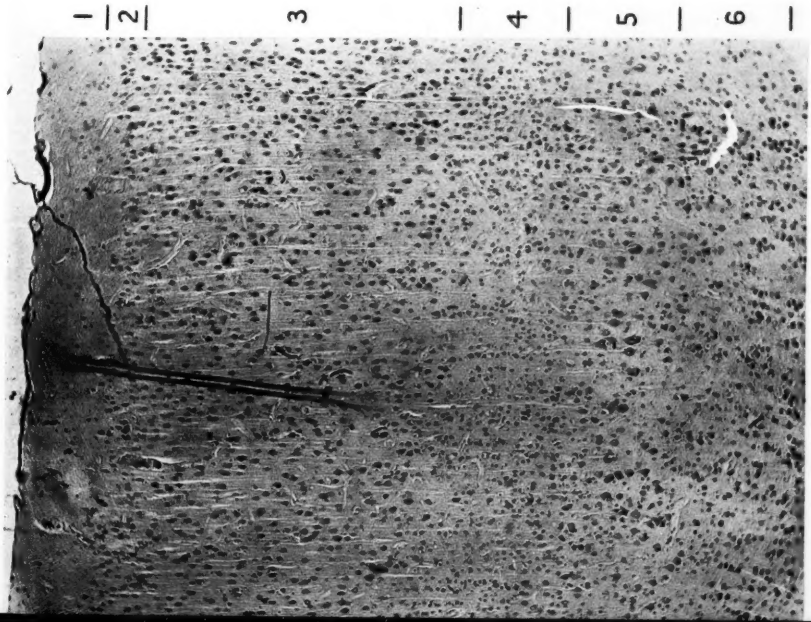

Fig. 3 (Area 5 and 7). Area Parietalis

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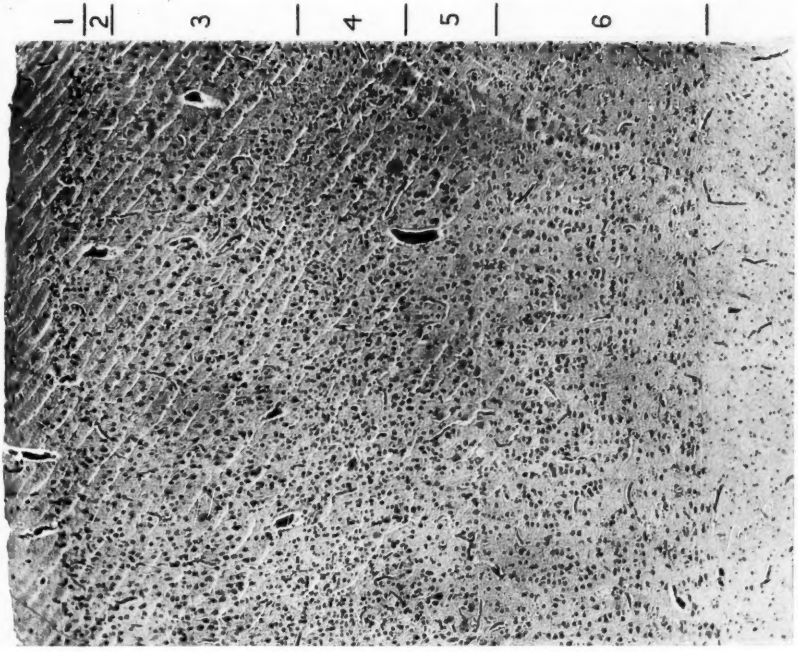

Fig. 6 (Area 18, 19). Area Occipitalis

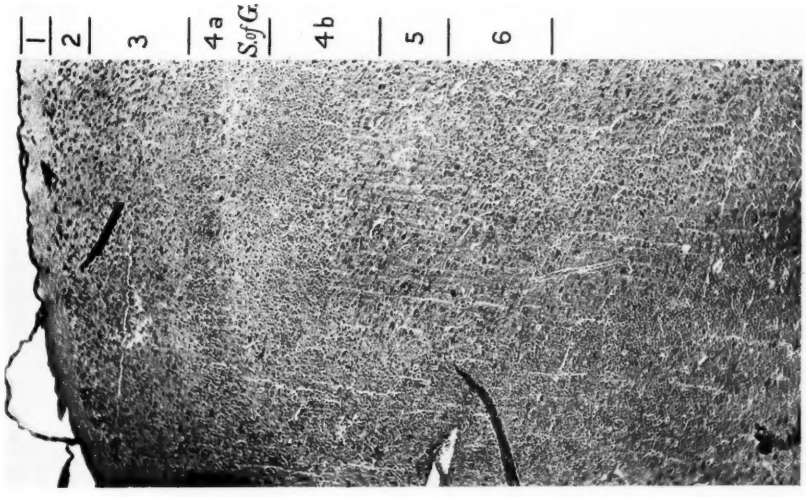

Fig. 5. Area Striata

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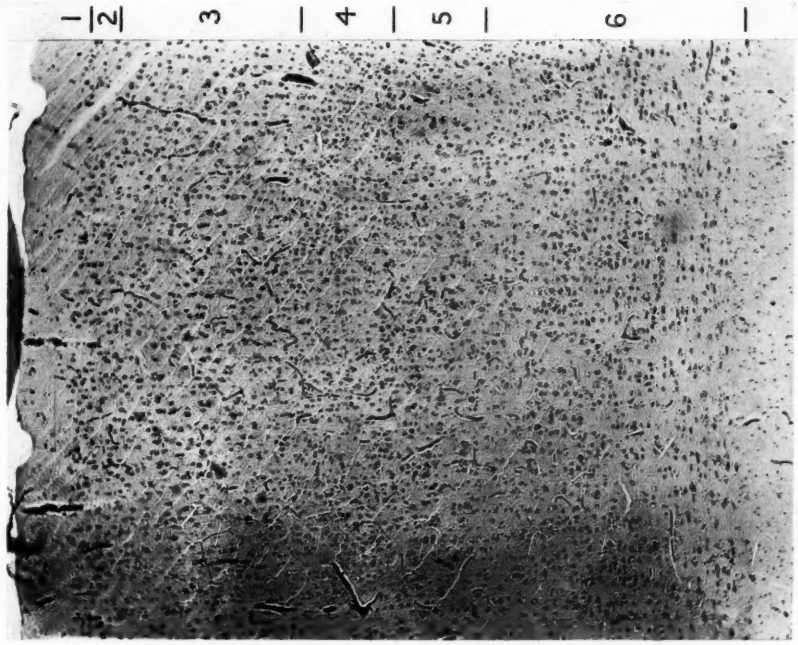

Fig. 8 (Area 20 and 21). Area Temp. Middle and Inferior

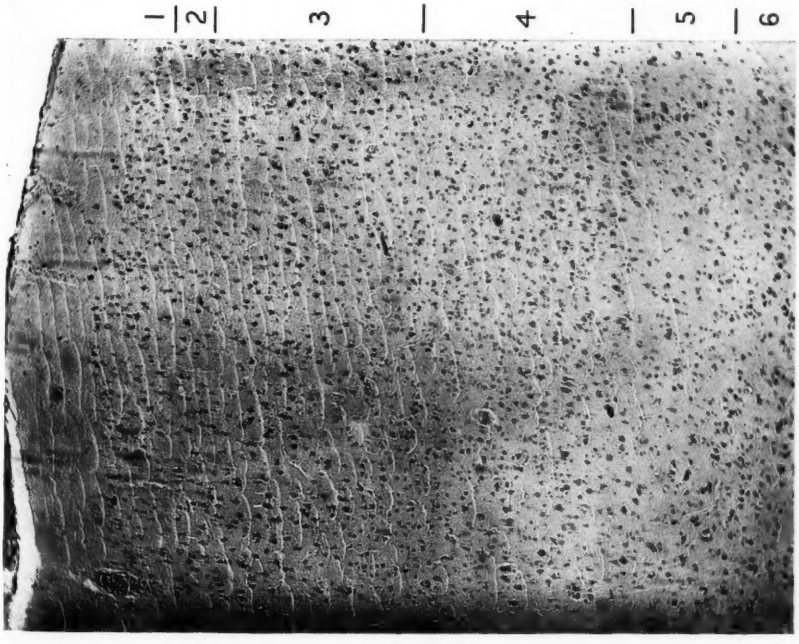

Fig. 7 (Area 22). Area Temp. Superior

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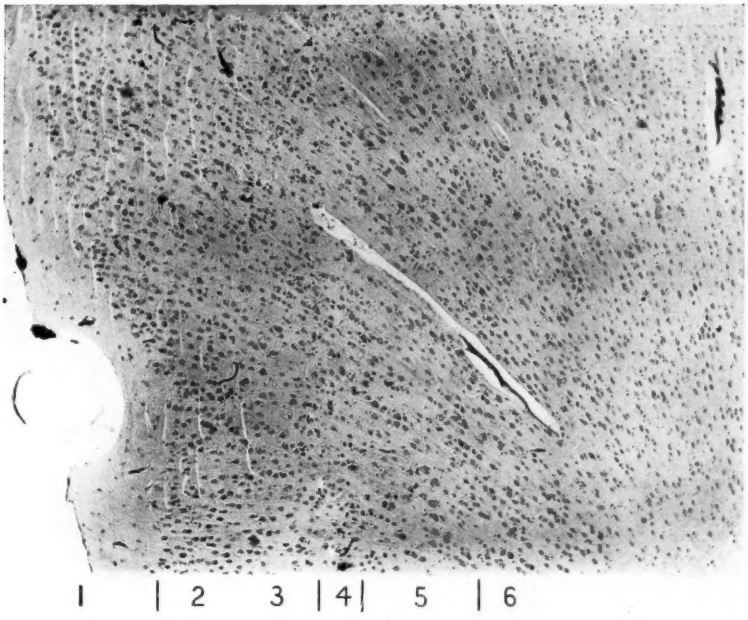
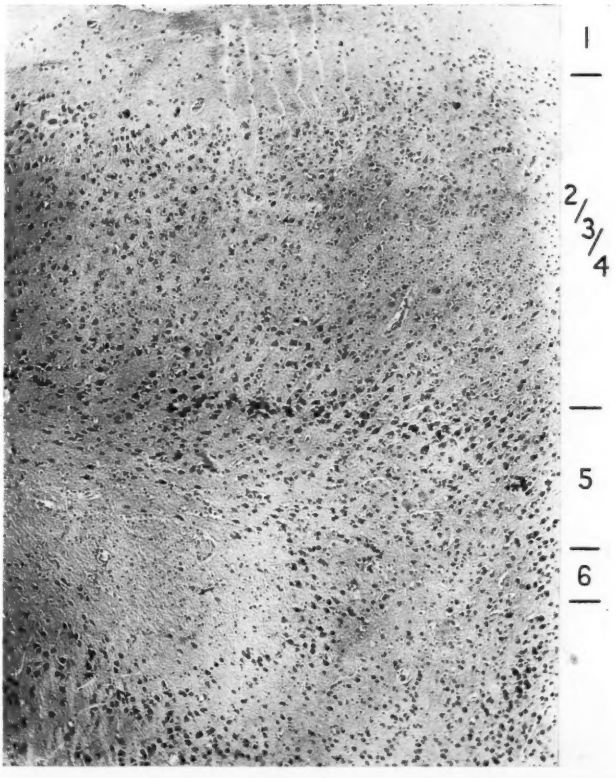


Fig. 9 (Area 24). Area Limbica



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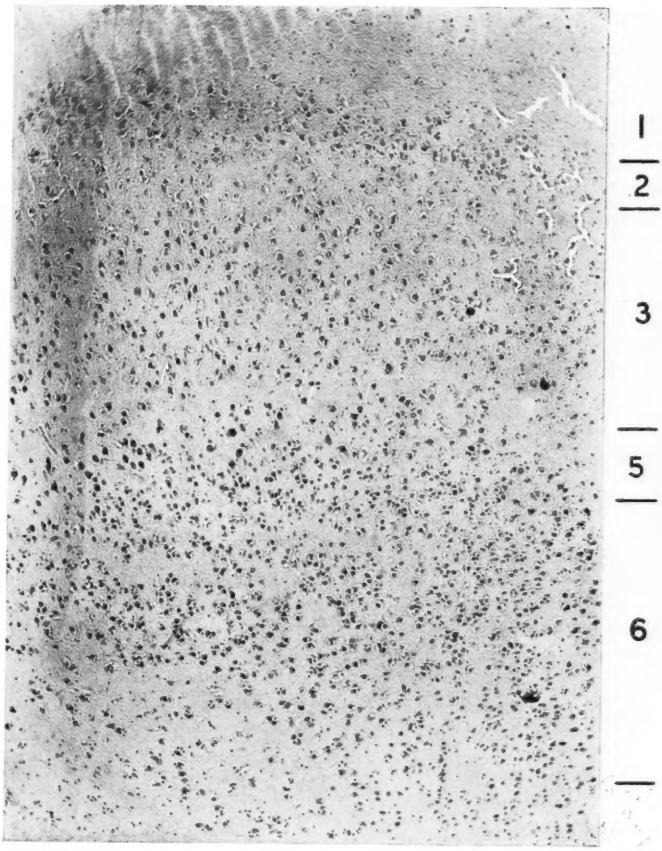

Fig. 11 (Area 27). Area Piriformis

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A SEPTDIGITATE FOOT IN MAN

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WHILE it is comparatively common to find in man supernumerary digits as an abnormality, these structures are usually in the form of tags of tissue resembling a normal digit in external form, and only rarely supplied with an osseous basis. One case is reported in which the individual possessed twelve toes on each foot and twelve and thirteen fingers on the hands[1]. In the limited library at my command in Singapore I can find no trace of any case of seven digits complete with metatarsals and the following case may be worthy of detailed description. The abnormality occurs on a Sikh youth of 16 years of age, resident in Singapore and is present on the left foot only. There is no history of any member of his family having this or any similar abnormality. There are seven complete and independent toes, the first and third toes closely resembling a normal great toe. Apparently the supernumerary digits are added on the medial side as the five lateral toes are, so far as appearance goes, the digits of a normal foot. The nails are well developed on all the toes and each of the toes is capable of independent action. In order to determine the osseous formation of the foot I had X-ray plates taken for which I have to acknowledge my thanks to Dr Webster, Radiologist to the General Hospital, Singapore. Fig 2 shows the arrangement of the tarsal and metatarsal articulations. To aid the reproduction of the photograph I have marked in the dorsal line of the articulations. From the photograph it will be seen that the cuboid is almost normal having two facets for articulation with two metatarsals, the facet for the seventh metatarsal having its axis directed more laterally than in the normal foot. While considering the angle of this surface it should be remembered that in the Asiatic this surface is normally more laterally directed than in the European, probably on account of the habit of squatting which the Asiatic never loses, the toes being then separated to their maximum, the weight of the body being chiefly borne on the heads of the metatarsals. The scaphoid is much larger than the normal bone and presents four facets anteriorly for articulation with four cuneiform bones. Coincident with the larger scaphoid, the head of the talus is larger in diameter than in the normal foot. The first cuneiform most closely resembles the normal bone. The second cuneiform is like a modified first, while the third and fourth resemble the normal second and third respectively, the abnormal third being

[1] ROSE and CARLESS. *Manual of Surgery.* 1916.
F. WOOD JONES in his *Principles of Anatomy as Seen in the Hand* also refers to Polydactylism.

Fig 1. Photograph to show the septdigitate foot. Note the resemblance of the 1st and 3rd toes to a normal great toe.

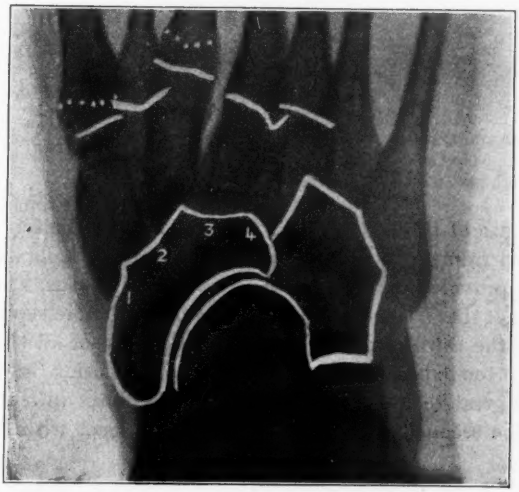

Fig. 2. X-ray photograph to show the tarso-metatarsal articulations (the photograph is reversed). The continuous white line shows the dorsal line of the joints, the dotted line, the epiphyseal plates of the 1st and 3rd metatarsals.

shorter than the second and fourth to receive the base of a metatarsal. Fig. 3 shows the arrangement of the metatarsals and phalanges. The first and third digits have each only two phalanges and the metatarsal shows the epiphyseal

Fig. 3. Skiagram showing the general arrangement of the osseous elements. Note that the first and third toes have each only two phalanges and the bones resemble those of a normal great toe. Both metatarsals are provided with sesamoid bones.

plate at the base of the bone (see also fig. 2), which definitely confirms the opinion formed from the external appearance that the hallux is duplicated. Both are also provided with sesamoid bones at their heads. The metatarsals and phalanges of the first toe are broader, heavier and more typical of a hallux than those of the third toe, but from a consideration of all the structures I believe the first toe to be supernumerary, the third toe being the representative of the normal great toe. The first metatarsal articulates with the first cuneiform, while the second articulates by an angular facet with both first and

second cuneiforms. The third metatarsal articulates with the second cuneiform, the fourth and fifth metatarsals with the third and fourth cuneiforms respectively, while the sixth and seventh metatarsals articulate with the cuboid. The second toe is obviously therefore the other supernumerary. All the toes are supplied with extensor tendons which can be palpated.

When first I observed the abnormality I was interested to know whether it might throw any light on the subject of the pre-hallux and post-minimal digit. In this specimen there is undoubtedly a pre-hallux complete with cuneiform. That this toe is not due to cleavage of a normal digit is indicated by the interposition of another digit between the hallux proper and the pre-hallux. Yet the supernumary digits must have been laid down early in intrauterine life as there is no indication of fusion between any of the bones. I am of the opinion however that the presence of these supernumerary digits is adventitious and while interesting as an anatomical abnormality has no morphological value.

THE ORGAN OF JACOBSON IN THE HORSE, OX, CAMEL AND PIG

By Capt. F. C. MINETT, M.B.E., B.Sc.
Royal Army Veterinary Corps

1. INTRODUCTORY

The organ of Jacobson has been carefully examined and described in a number of animals. It has been found to exist in all the mammals which have been examined (Symington (1891), von Brunn (1892), Klein (1881), Read (1908) and others), but it is not confined to this class as among reptiles the structure is present in a well-developed state in many lizards and snakes and among certain of the higher amphibians also. It reaches its highest development however in certain Monotremes such as *Ornithorhynchus*, *Echidna*, *Monitor* (Broom, 1895). In man it is rudimentary while in Carnivores and Herbivores it is well developed. The importance of the organ from the point of view of zoological classification has been suggested by Broom (1897). A short summary of existing knowledge on the subject will be found in a small text-book by Parker (1922).

Strange as it may appear, in the literature on the subject there is a curious lack of reference to the organ in the horse, and no very close description of it has appeared, though the structure has no doubt been examined many times. The older text-books of veterinary anatomy give hopelessly inaccurate accounts while in some of the newer works, which are of course primarily intended for students and practitioners, the accounts are usually confined to four or five lines.

I have not found any description of the structure in the camel.

Acting on a suggestion by Major-General Sir F. Smith, K.C.M.G., it was resolved to attempt a closer examination of the structure in certain mammals which were available.

2. GENERAL DESCRIPTION OF THE ORGANS

The organs are to be found on the floor of the nasal cavity beneath the mucous lining and on each side of the base of the septum. They are tubular in form, ending blindly posteriorly while anteriorly they join the nasopalatine canals and in this way communicate with both the nose and the mouth. In its highest development the organ extends anteriorly beyond this canal for some distance to end blindly or it may even extend into the lateral cartilages of the nose as in some lizards (Broom, 1895). The tube is a mucous one with a sensory epithelial lining, olfactory in function, and is invested partially or

completely by a sheath of hyaline cartilage. In section the lumen of this tube is usually found to be kidney-shaped or half-moon shaped.

3. THE ORGAN IN THE HORSE

The organ is comparatively well developed in the horse, being 12–13 cm. long in an animal of medium size, the posterior blind extremity being thus about level with the second premolar tooth. Its cartilaginous sheath lies in a groove formed at the junction of the vomer with the symphysis of the palatine processes of the superior maxillary bones and is closely applied to the bony tissue, especially anteriorly where the grooves deepen.

If sections be made of the organs at different levels it is seen that the lumen varies in size and shape. Thus at any point along the posterior seven-eighths the lumen is revealed as a crescentic slit about 3 mm. in extent, the concavity being to the outer side. Anteriorly the lumen becomes circular and constricted

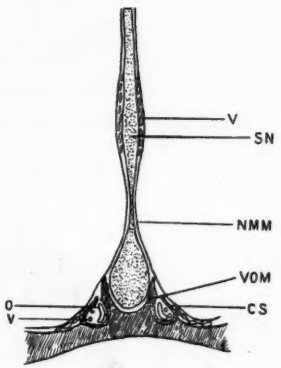

Fig. 1.

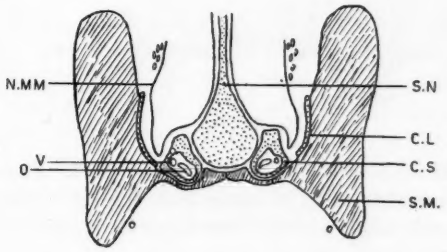

Fig. 2.

to a diameter of 1 mm. where it communicates with the nasopalatine canal by an elliptical opening on its inner wall, the opening being about 1 cm. from the nasal extremity of the canal.

The nasopalatine or Stenson's canal is about 3 cm. in length, the posterior opening being at the extreme anterior corner of the floor of the nasal fossa about 5 cm. behind the lachrymal opening, whence it is directed downwards and forwards to end blindly in the cartilage filling the incisor cleft. The failure of this canal to form a complete channel between the nose and the palate in the horse is to be particularly noted as this is exceptional. A distance of about 1 cm. separates the blind end of the canal from the surface of the hard palate.

In the published accounts of Jacobson's organ, a good deal of stress has been laid on the arrangement of the investing cartilage, this being essentially different in the Prototheria and in the Eutheria. In the horse for the greater

part of its extent the cartilaginous covering conforms to what is the usual type in Eutheria as may be seen in fig. 1, in which the relation to the vomer and the shape and position of the organ may also be noted. Posterior to this the tube in places is extremely thin or entirely absent at its floor, the outer wall being quite independent of the inner at that point. For a short distance anteriorly the cartilaginous covering becomes a complete tube (fig. 2) and here it joins a cartilaginous lamella placed on the inner wall of the superior maxilla.

Fig. 3 shows Stenson's canal in section close to its blind extremity. Fig. 4 represents the face of a section taken about 1 cm. anterior to fig. 3; therefore, by comparing the two it will be seen that the cartilage covering Jacobson's organ is continuous anteriorly with the expanded base of the septum nasi where this rests upon the palatine processes of the premaxillary bones and

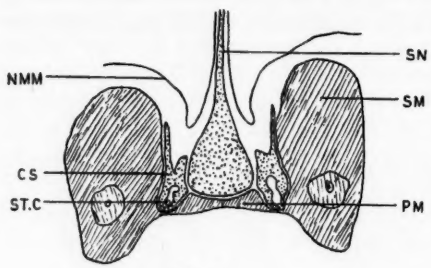

Fig. 3

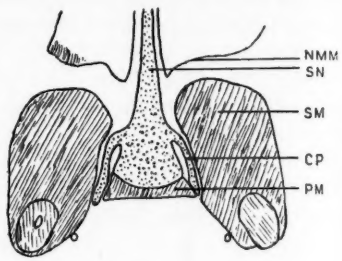

Fig. 4

with the cartilage of the incisor cleft. Posteriorly the tube first becomes incomplete as to its outer wall, the inner wall persisting for some 4 or 5 cm. further back where it maintains its position in the shallow depression on the outer surface of the vomer.

No essential differences are to be observed in the structure in the ass and mule.

Nerve Supply

This is from two sources, olfactory and sphenopalatine, the innervation thus being similar in part to that of the nasal mucous membrane as a whole. Read (1908) describes in the dog the anterior ethmoidal nerve as supplying the organ also. This nerve no doubt corresponds with the nasal branch of the ophthalmic (M'Fadyean). I have not been able to trace the fibres of the latter nerve as far as the organ in any of the animals here examined.

Olfactory. These can mostly be seen without dissection on the deep face of the septal mucous membrane (beneath a thin fibrous sheet) on carefully stripping this from the cartilage, where they appear as thin greyish bands descending downwards and forwards from the region of the lateral masses. Many of these are extremely fine and are lost in the mucous membrane. The fibres however which reach Jacobson's organ are mostly derived from one rather broad band which takes its origin from the posterior surface of the

olfactory lobe. This branch passes inwards to enter a bony canal in the crista galli process, on emerging from which it lies for 2 or 3 cm. in a groove on the surface of the mesial ethmoidal plate. It enters the organ 2 or 3 cm. from its upper extremity and its fibres can be traced nearly as far as its nasal opening.

Sphenopalatine. This nerve issues from the sphenopalatine foramen in company with the artery and vein of the same name, and immediately divides into an outer and inner branch. The latter passes to the deep surface of the septal membrane where 3–5 cm. from its origin it divides into a number of small trunks which gradually diverge. Of the more superior of these one or more penetrate the organ, the others being distributed to the septal membrane. A larger inferior branch enters a bony canal in the side of the symphysis of the hard palate (where it accompanies branches of the palatolabial artery) whence it is eventually distributed to the palatal membrane behind the incisor teeth.

Blood Supply

No vessels of any considerable size are to be found entering the organ. No doubt blood is received from at least two of the sources which supply the nasal cavity, viz., sphenopalatine and palatolabial.

Text-books of veterinary anatomy do not refer to the latter vessel supplying blood to the nasal cavity. It does so however through a branch which is usually given off from the left, though sometimes from the right, palatolabial artery about 4 cm. below the first premolar tooth. This branch passes obliquely upward to enter a bony canal in the symphysis of the palatine plates of the superior maxillae at their junction with the vomer, where it subsequently divides into two. Twigs from these two branches are to be found embracing the cartilage of the organ at intervals of its length—usually on its outer aspect—where they are distributed in the septal mucous membrane. It seems that "nasopalatolabial" would be a better designation for this artery in the horse.

Accompanying the organ are constantly to be found one or two veins which increase in calibre as they pass backwards to join the sphenopalatine vein.

THE ORGAN IN THE CAMEL

The organ measures 15–16 cm. in length in the adult, and so is relatively longer than that in the horse which it resembles in general arrangement.

The tube is narrowest in its anterior third where its lining is black pigmented; posteriorly it is more dilated and in section presents the usual reniform appearance (fig. 5). Anteriorly it opens into the nasal cavity above but in close proximity to the nasal opening of Stenson's canal. It does not open clearly into the canal of Stenson as in the horse. The nasal orifice of Stenson's canal is oval and about 6 mm. in its long vertical diameter (fig. 6) The canal is continued downwards and forwards through the incisor cleft for 2–3 cm. where it ends blindly about 1 cm. from the surface of the hard palate.

The investing cartilage is roughly similar to that in the horse but differs from it in being complete inferiorly and incomplete superiorly throughout its whole extent. Posteriorly its inner portion extends 1–2 cm. further back than

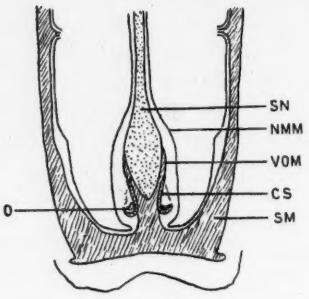

Fig. 5

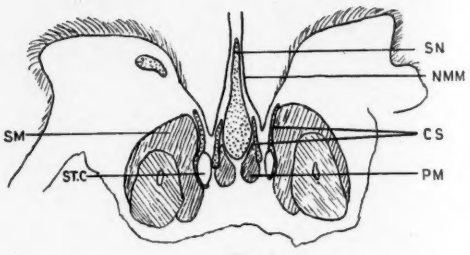

Fig. 6

the outer and the blind extremity of the organ. Anteriorly the outer portion of the tube is again lost before the inner and from fig. 6 it may be seen that the wall of Stenson's canal is supported outwardly by a cartilaginous lamella lining the inner wall of the premaxillary bone. At about this point too the persisting inner wall is connected to the base of the septum nasi.

Nerve Supply

Two bands of grey olfactory fibres can be seen passing forwards on the deep surface of the septal membrane from the region of the lateral masses, the lower of these being the larger. Both bands pass through the cleft at the upper border of the cartilage sheath and can be traced to the anterior third of the organ which they supply.

The sphenopalatine nerve can be distinguished as being whiter than the olfactory bands. It has much the same disposition as in the horse. A larger portion of the inner branch descends below the cartilage of the organ to supply the palatal membrane, the remainder supplies the nasal mucous membrane, and one small branch enters the organ.

Blood Supply

From the sphenopalatine artery. An important branch of this artery accompanies the inner branch of the nerve of the same name to be finally distributed to the palatal membrane. Branches from this vessel, which include one to the organ, supply a large part of the septal membrane where some appear to anastomose with descending branches of the nasal branch of the ophthalmic artery. No large vein accompanies the organ as in the horse.

THE ORGAN IN THE OX

Specimens were examined from adult cattle of the native Egyptian and Cyprus breeds, in both of which the structures were very similar. The organ

is comparatively short and broad, the length being only 8 or 9 cm. The lumen in transverse section appears as a crescentic slit as much as 7 mm. in extent, the concavity being outwards. Posteriorly the tube maintains this shape as far as the blind end but in the anterior third it becomes considerably constricted (about 3 mm.). In the Egyptian ox it opens into the nasopalatine canal about 1 cm. from the nasal opening as in the horse, but in the Cyprus ox this opening is slit-like and only about 1 cm. from the palate. In one ox the length of the organ from the blind end to the anterior opening was nearly

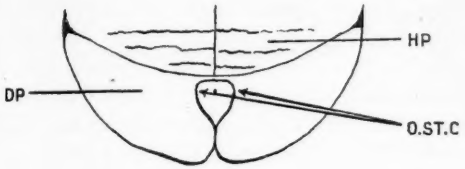

Fig. 7

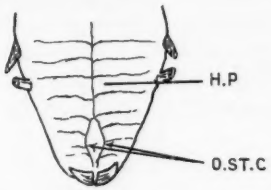

Fig. 8

12 cm. the organ running in company with the nasopalatine canal for 3·5 cm. before opening into it. The nasopalatine canal in these species forms a complete tube (5 or 6 cm. long) between the nose and the mouth, the nasal opening, which is widely dilated, being situated in the extreme anterior corner of the floor of the cavity. The buccal opening, which is very constricted, is located at the bottom of a groove which encloses a heart-shaped area on the dental pad at the position shown in fig. 7.

The arrangement of the investing cartilage is as follows. At its centre it forms a complete tube, posteriorly it becomes more and more incomplete along its upper aspect to gradually disappear at a point 4 or 5 cm. above the blind end. Towards the anterior extremity the cartilage becomes incomplete on its outer side.

The nerve supply is similar to that in the horse.

THE ORGAN IN THE PIG

The specimen examined was that of a very young pig, the head measuring 14 cm. long, while the organ was 2·3 cm. long, extending as far back as the level of the first premolar tooth.

The general arrangement of the organ and its cartilage may be seen in fig. 9. The lumen in section about its middle is slit-like, the slit being concave on its outer side. The cartilage is incomplete throughout; anteriorly it blends with that of the septum nasi; posteriorly its inner wall persists alone for a few millimetres beyond the blind end of the organ. The opening into the nasopalatine canal is relatively close to the palate, and the common ducts open on the palate in the positions shown in fig. 8. A fine bristle may be passed into each of these openings.

Two fine olfactory nerves may be seen coursing on the deep face of the

septal membrane to enter the organ which is also supplied with a small branch from the sphenopalatine.

4. HISTOLOGICAL

In a transverse section as seen under the low power (displayed diagrammatically in fig. 10), the position of the parts is as follows. The lumen of the organ is slit-like with the outer portion of the lining pushed into a concavity of the inner, this lying in close proximity to the cartilage sheath. The olfactory

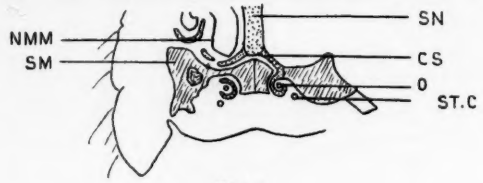

Fig. 9

nerve bundles are situated beneath the inner lining towards the upper aspect, while the sphenopalatine nerves and vessels are embedded in the connective tissue to the outer side of the tube. Numerous glands of the racemose type are also present in this connective tissue and are largely congregated around the extremities of the slit.

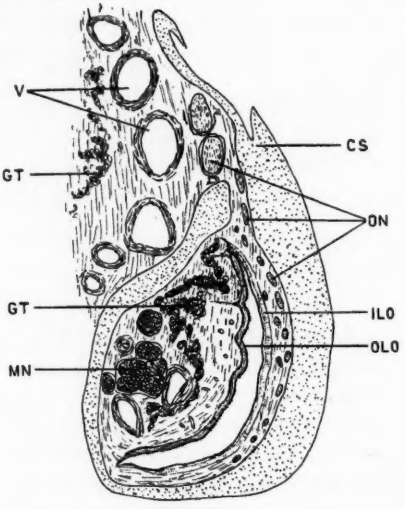

Fig. 10

In sections from almost any part of the organ (except perhaps the anterior fifth) it is possible to distinguish the outer portion of the lining from the inner, that being respiratory and this olfactory in type. In the horse the inner lining, which is rather thicker than the outer, is formed of a layer of columnar

cells the protoplasm of which in haematein and eosin preparations stains rather faintly in comparison with that of the outer. Between these may be seen a good many goblet cells and small lymphocytoid cells set on a deeper stratified layer. The surface of this portion always shows a quantity of adherent mucus.

In the outer lining the superficial cells are ciliated and set upon a layer of stratified cells with somewhat elongated nuclei. The distinction between the two classes of epithelium may be seen very clearly in eosin-Löffler methylene blue preparations in which the proper degree of differentiation with weak acid-alcohol has been attained. In the outer portion the nuclei of the basal cells stain rather diffusely and of a deep purple tint and are in sharp contrast to the nuclei of the ciliated cells, the nucleoli of which alone retain a distinct blue tint. In the inner lining the purple-staining basal cells are not present, the nuclei of the whole layer staining blue and not diffusely.

At the junctions between the two portions the lining is gradually thinned, the epithelium becoming cubical and finally almost flattened. It is in this situation that most of the ducts of the racemose glands open.

The lining of the nasopalatine canal is formed of two or three layers of flattened, pavement-like cells with oval nuclei and in the supporting connective tissue racemose glands are abundantly present.

In the other animals examined the histological features were essentially similar. In all the olfactory function appeared to be confined to the inner portion of the lining. In the bovine the organ becomes considerably constricted anteriorly where the whole lining seemed to be olfactory in type. The nasopalatine canal in this species is lined by stratified, squamous epithelium resembling that of the mouth. This epithelium is papillated, the papillae containing a network of capillaries, and in the connective tissue wall are numerous glands with ducts opening on the surface.

5. PHYSIOLOGICAL

As nothing very precise is known regarding the physiology of the organ, a few words on the subject will not be out of place.

Firstly, there can be no doubt but that the function of the organ is olfactory. The difficulty about the matter however is to understand how this function is exercised when one bears in mind that the anterior part of the tube is constricted and that the orifice is usually placed in a comparatively inaccessible position in the nasal cavity. Again it may be asked, what is the necessity for the provision of such a specialised organ of smell?

It was suggested (1) to measure the pressure required to bring about inflation of the tube, (2) to search for the mechanism which during life might lead to such inflation and so bring air into contact with the olfactory cells.

By introducing a small cannula into the nasal opening of Stenson's canal in a fresh specimen (horse) and exerting gentle air pressure it was found to be quite an easy matter to inflate the organ, a pressure of about 40 mm. mercury

sufficing. The degree of inflation could be appreciated by noting the rise and fall of the nasal mucosa covering the cartilage sheath when the air pressure was varied. It should be noted that the end of the cannula was inserted into the nasal orifice of Stenson's canal and not actually into the orifice of the organ of Jacobson. A careful search in the organ in the horse was made for striped or unstriped muscular tissue which presumably might cause dilatation of the tube during life. Attention was especially directed to the anterior portion of the organ since it is here that one might expect any dilating mechanism to be best developed. While it can certainly be said that no striped muscle was encountered, one cannot be quite so dogmatic as to the presence or absence of unstriped muscle. However, except in one instance and apart from vessels there was no obvious stratification of these muscle cells, though no doubt they exist in the abundant connective tissue on the outer aspect of the organ. While therefore the organ may be easily inflated from the nasal cavity by artificial means, the exact manner in which air is brought into contact with its lining cells during life remains uncertain.

My sincere acknowledgments are due to Dr W. H. Wilson, Professor of Physiology in the School of Medicine, Cairo, for helpful advice respecting the concluding section of the work. It is unfortunate that for certain reasons I was unable to carry out all his suggested experiments.

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REFERENCES TO FIGURES

O = Organ of Jacobson.
CS = Cartilaginous sheath.
ST.C = Stenson's canal.
SN = Septum nasi.
NMM = Nasal mucous membrane.
V = Vein.
VOM = Vomer.
CL = Cartilaginous lamella.
SM = Superior maxilla
PM = Premaxilla.
CP = Cartilaginous prolongation of septum nasi
HP = Hard palate.
DP = Dental pad.
O.ST.C = Opening of Stenson's canal.
GT = Gland tissue.
MN = Medullated nerves.
ON = Olfactory nerves.
ILO = Inner lining of organ.
OLO = Outer lining of organ.

A RARE CASE OF TORTUOSITY OF THE INTERNAL CAROTID ARTERY

By ALEJANDRO RODRIGUEZ CADARSO, *Professor of Anatomy*, and JUAN JOSÉ BARCIA GOYANES, *Assistant-Professor of the University of Santiago (Spain)*.

In an interesting paper on the "Tortuosity of the Cervical Segments of the Internal Carotid Artery," published in the *Journal of Anatomy*, vol. lix, Part I, Dr John Cairney of Otago records the results of his observations in adults and foetuses and discusses the causative factors of the condition.

Without adding further to the discussion we wish to confirm Dr Cairney's observations by stating that in our experience the internal carotid artery sometimes displays marked tortuosity, if not in the foetus at any rate in children under five years of age, and that we have found no evidence that the condition was associated with disease.

Dr Cairney reduces the various forms of tortuosity he has observed to three main types, but notes that, in addition to these, other types have been

Fig. 1

recorded. He refers particularly to a remarkable case recorded by G. M. Smith in 1902, in which the vessel formed a complete circular coil.

Nearly seven years ago one of us together with Professor S. Guisande of Seville University presented a note to a Medical Congress describing a similar case of this rare and interesting condition, which at the time we regarded as unique as we were unaware that it had been recorded previously.

As may be seen in the accompanying figure taken from a cast of a dissection now in our museum the left internal carotid artery, one centimetre below the inferior opening of the carotid canal, was disposed in a complete coil in the sagittal plane and was in appearance comparable with the coiled part of a manometer tube.

APPOINTMENTS

UNIVERSITY OF ABERDEEN

Dr ALEXANDER LOW, Lecturer on Embryology in the University of Aberdeen, has been appointed by the Secretary for Scotland to the Chair of Anatomy in succession to Prof. ROBERT W. REID. Prof. Reid has held the Chair for thirty-six years, having been appointed in 1889 in succession to Prof. Sir JOHN STRUTHERS. His successor, Dr Alexander Low, is well known as the author of important papers on Embryology and Anthropology.

UNIVERSITY COLLEGE, DUNDEE

The post rendered vacant by the retirement of Principal YULE MACKAY, M.D., from the Chair of Anatomy in University College, Dundee, was filled by the University Court of St Andrews University on September 15th by the election of Dr D. R. Dow. The new Professor was medallist in most of the Medical Classes at St Andrews University, and graduated with distinction. Thereafter he gained the Diploma in Public Health, and was awarded the degree of M.D. with distinction. He held resident appointments in the Dundee Royal Infirmary and in the Hospital for Sick Children, Great Ormond Street, London. During the war he held a commission in the R.A.M.C. Since 1913 he has been Lecturer on Regional Anatomy at the United College and assistant successively to Prof. Musgrave and Prof. Waterston, the Bute Professors of Anatomy there. His published works include: *The Anatomy of Rudimentary first Thoracic Ribs with Special Reference to the Arrangement of the Brachial Plexus, The Incidence of Arterio Sclerosis in the Arteries of the Body, Spontaneous Rupture of the Heart.*

Dr Dow has carried on general practice at Crail, first in association with his father, the late Dr Dow of Crail, and after the death of the latter independently.

Dr Dow is thirty-seven years of age.

Part I of Vol. LIII of the *Journal of Anatomy*, which has for some time been out of print, has been reprinted and can be supplied at 10*s*. net.

A CONTRIBUTION TO THE STUDY OF THE MODERN EGYPTIAN CRANIUM

By SYDNEY SMITH, M.D., D.P.H.

Principal Medico-legal expert, Egyptian Government

In Egypt, where there is a mixture of races and where murder and secret disposal of bodies is a common occurrence, it is frequently necessary in medico-legal practice to give an opinion as to the racial origin of a skull or skeleton.

The problem which confronts one is usually to decide whether the remains are those of a European, Egyptian or Negro.

Though there are many published reports on the measurements of Negro, European and ancient Egyptian crania there are none on modern Egyptians. With the object of obtaining data for the crania of the latter and in order to ascertain whether there were any characters in the Egyptian skull which might aid in its identification, I measured a number of skulls which came into my hands in connection with various crimes.

In the first series of 21 skulls acquired, very distinct racial characters were found, especially with reference to the height, length of base, and relationship between height and breadth.

The height in this series had an average of 140 mm., which was higher than any known series of measurements of modern crania, while the length of the base (basi-nasal) gave an average value of 105 mm., again much longer than any other race.

As these skulls were all from known persons and as they were the total number collected without excluding any specimen, there was no apparent possibility of selection and they appeared to be a typical random sample. They were mixed Copts and Moslems and as far as could be judged there was little difference between the two sects.

It appeared, therefore, that there were certain definite racial characters in the Egyptian skull, and the material acquired interest on anthropological grounds. A series of measurements were therefore made as suggested by the Frankfort concordat, using the same nomenclature for ease in comparison with other series of measurements. The following measurements were taken, the methods followed being those described by Fawcett (*Biometrika*, vol. I, p. 426):

L greatest length from glabella to occiput.
B greatest transverse breadth.
B′ least frontal diameter on the temporal lines.
H height from basion to bregma.

OH auricular height by means of the craniophore, the skull being placed in the Frankfort plane.
LB skull base from basion to nasion (basi-nasal).
GL from basion to alveolar point (basi-alveolar).
G'H upper facial height from nasion to alveolar point.
GB breadth of face from the lowest points of the malar-zygomatic sutures.
NH nasal height from nasion to lower margin of nasal aperture.
NB greatest breadth of nasal aperture.

The following indices were also calculated:

100*B*/*L*, *H*/*L*, *H*/*B*, *B*/*H*, *G'H*/*GB*, *NB*/*NH*, *GL*/*LB*, *L*/*LB*, *B'*/*GB*.

An endeavour was made to obtain a longer series, for it was obvious that in a short series of 21 skulls there was liable to be a considerable error if any proportion of them happened to show a marked deviation from the normal. Although it was impossible to obtain many known skulls I managed to take the measurements of another lot of 30 supposed male skulls from a modern Coptic cemetery. The sex of these was unknown and they had to be sexed by anatomical appreciation. The sexing of skulls is an extremely difficult operation, and in a number of skulls it is quite impossible for the most expert anatomist to decide whether they are male or female. This group of 30 therefore contained a few skulls which I accepted as male, but in which the male characters were by no means distinct.

The means of the measurements of the two series were as follows:

	L	*B*	*B'*	*H*	*OH*	*LB*	*GL*	*G'H*	*GB*	*NH*	*NB*
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
1st group	187	134·4	94·4	140	118·8	105·3	100	70	95·7	51·4	25·9
2nd group	183·6	131·2	92·9	135·1	—	103·1	98·5	68·96	92·1	50·35	25·27

It will be observed that the measurements as a whole are reduced in the second group but preserve the same relationships as is shown by the following indices:

	100 *B*/*L*	100 *H*/*L*	100 *GL*/*LB*	100 *G'H*/*GB*	100 *NB*/*NH*	100 *L*/*LB*
1st group	71·09	74·25	94·96	73·3	50·4	177·6
2nd group	71·4	73·57	95·10	74·87	50·2	178·1

During the time that these were under examination I obtained seven male skulls of known origin and thought it advisable to group the whole series of 58 together and from this mixed group I obtained the following mean values. (The individual measurements are given in the appendix attached hereto.)

L	*B*	*B'*	*H*	*LB*	*GL*	*G'H*	*GB*	*NH*	*NB*
mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
184·52	132·56	93·65	137·09	103·89	99·02	69·03	93·53	50·64	25·10

In this mixed group the same outstanding characters are observed, namely, the height, length of base and relationship between height and width.

COMPARISON WITH ANCIENT EGYPTIAN SKULLS

For the purpose of comparison with ancient skulls of the same race I have selected the measurements given in *Biometrika* (vol. I, p. 426) of Prehistoric

Egyptians measured by MacIver, Naqadas measured by Fawcett, and late dynastic Theban Mummies taken from the German anthropological catalogue.

A comparative table of the means of these three series with my modern Egyptians is given herewith:

	Prehistoric Egyptians	Naqadas	Theban Mummies	Modern Egyptians
L	184·50 mm.	184·13 mm.	181·94 mm.	184·52 mm.
B	132·38 „	134·87 „	136·63 „	132·56 „
B′	—	91·06 „	93·83 „	93·65 „
H	133·94 „	135·21 „	136·05 „	137·09 „
OH	—	115·59 „	114·34 „	118·8* „
LB	100·92 „	99·34 „	100·63 „	103·89 „
GL	96·12 „	94·72 „	95·79 „	99·02 „
G′H	70·64 „	67·59 „	68·78 „	69·03 „
GB	—	95·85 „	95·66 „	93·53 „
NH	50·36 „	48·94 „	50·61 „	50·64 „
NB	25·10 „	25·12 „	25·26 „	25·10 „
100 *B*/*L* ...	71·78	72·99	75·07	71·84
100 *H*/*L* ...	72·60	73·30	74·71	74·29
100 *H*/*B* ...	101·18	100·47	99·64	103·3
100 *B*/*H* ...	98·84	99·76	100·36	96·711
100 *G′H*/*GB* ...	—	70·6	72·3	73·80
100 *NB*/*NH* ...	50·03	51·1	50·1	49·57
100 *GL*/*LB* (Gnathic)	95·2	95·4	95·2	95·31
100 *L*/*LB* ...	182·8	186·4	180·8	177·6
100 *B′*/*GB* ...	—	95·0	98·1	100·12

* *OH* on 21 only, of which *H* = 140 mm.

This table brings out some remarkable features, for practically every dimension of the modern Egyptian skull corresponds closely with those of the prehistoric race with the exception of the height and the basal length. This is of extreme interest, for in the intermediate period, there have been considerable changes in the shape of the skull.

For example, the *width* of the prehistoric skull, 132·4 mm., rose to 134·8 in the Naqadas, 136·6 in the Theban Mummies and reached a figure of 139 mm. in the pyramid builders of the 4th–6th Dynasties at Giza, a breadth which was found also in the 6th–12th Dynastic skulls in Upper Egypt (*Bulletin No.* 6, Nubian Survey, p. 16).

The increase in width is attributed by Elliott Smith and Derry to the influx of aliens into Egypt in the early dynastic times, and the increase in diameter was associated with other distinct changes in the skull and skeleton. If, as they assume, it was a racial admixture which altered the form of the skull, it appears to have produced its maximum effect between the 4th–12th Dynasties and in the process of time its effect became gradually eliminated and the skull of the Egyptian of to-day has reverted to the original width of his predecessor of prehistoric times.

These observers pointed out *apropos* of the reduction in width during the Ptolemaic-Roman period to 135·7 mm. (*loc. cit.* p. 25): "The Egyptian people from the early dynastic period onwards has shown an extraordinary capacity of assimilating a vast mass of alien population unto itself and at the same time of retaining its own distinctive peculiarities."

This remark is interesting in view of the further reduction of the width of

the skull from Roman times to the present, when it has attained the dimensions of the prehistoric skull. This point will be considered in greater detail later.

The *length* of the skull (184·5 mm.) has not altered to any appreciable extent in the six or seven thousand years, and to-day reaches the same figure of 184·5 mm.

Forehead. The least breadth of forehead (93·6 mm.) has increased by 2·6 mm. over the early dynastic skull but remains practically the same as in the Theban Mummies (93·8 mm.), and is still perhaps the smallest forehead measurement of any known race.

	Egyptian	Negro	French	German	English
Forehead (*B'*)	93·6 mm.	95·9 mm.	96·2 mm.	97 mm.	98 mm.

Height (basi-Bregmatic). The height shows a fairly regular and consistent increase from the prehistoric figure of 134 to 135 mm. in the Naqadas, 136 mm. in the Theban Mummies and 137 mm. in the modern Egyptian. This increase in height has considerably altered the relative measurements of the skull, for whereas the breadth was previously greater than the height we have now an excess of height over breadth of 4·5 mm.

This relationship has always been considered a primitive feature in skulls, but whether we are justified in this assumption is a moot point. Certainly in the Negro there is a tendency for the height to be equal to, and occasionally to be greater than, the breadth, and in primitive skulls in general there is a tendency to increased height, but I am not aware of any measurements of any race in which there is an excess of height over width such as I have shown to exist in the modern Egyptian skull.

An excessive height is a feature of ancient English (Longbarrow) and other stone-age skulls, but even in these the breadth is always greater than the height (Macdonell, *Biometrika*, vol. III, p. 243).

	Longbarrow (MacAlister)	Swedish stone-age	Aino	Reihengräber Schädel	Modern Egyptians
H	137 mm.	138 mm.	139·5 mm.	140·5 mm.	137·1 mm.
B	140 „	142 „	141·2 „	142 „	132·6 „

Karl Pearson has drawn attention to the importance of the height-breadth relationship from a racial point of view and has evolved an index which he calls the acroplatic index ($100\ B - H/L$) in which the various races appeared to fall into some sort of racial order, with the modern Europeans at one end of the scale, the Negroes at the other, and the prehistoric and primitive races in the centre.

Acroplatic Index. Males

Wurtembergers ...	+9·5	Gaboon (1864) ...	+0·0
Bavarians	+9·0	Kaffir	+0·0
French	+7·2	Aino	−0·1
English (Moorfields)	+7·1	Naqada	−0·3
„ (Whitechapel)	+4·2	Predynastic Egyptians	−0·5
Congo	+2·6	Zulu	−0·7
Longbarrow	+2·2	Angoni	−1·2
Egypt 4th Dynasty ...	+1·5	Modern Negro ...	−1·3
Gaboon (1880) ...	+0·9	Modern Egyptians ...	−2·47
Theban Mummies ...	+0·4		

In the modern Egyptian, however, the acroplatic figure falls far below zero (– 2·5) and this low acroplatic figure marks the Egyptian skull in a most distinctive manner. *There is no other known race in which this index falls so far below zero.*

It is an interesting speculation as to the reason for this steady increase in height of the Egyptian skull. It cannot be assumed to be entirely due to Negro admixture for the height is relatively much greater than in the Negro. There is, however, strong reason to believe that there has been considerable admixture with Arab blood and the Arab has a typically high skull. If, as is suggested, excessive height is a primitive feature, there is every possibility that it would be retained in the offspring of mixed people much more readily than less primitive features and therefore while other characters have been absorbed and eliminated the excessive height has been retained. In this character therefore the present-day Egyptian must be considered more primitive than his prehistoric ancestor.

Basal length. The length of the base from the basion to the nasion shows an increase from 100·9 mm. in the prehistoric skull to 103·9 mm. in the modern cranium although there was a tendency to a reduction of this length in the intermediate period (99·3 and 100·6 mm. in the Naqadas and Theban Mummies).

The increase is most significant for an excessive basal length is a distinctly negroid character. Associated with this increased basi-nasal length there is an almost equal increase in the basi-alveolar length (*GL*) from 96·12 mm. to 99·02 mm. in the same period and this measurement also shows a diminution in the intermediate period.

	Prehistoric Egyptians	Naqadas	Theban Mummies	Modern Egyptians	Modern Negro
(*LB*) Basi-nasal	100·92 mm.	99·34 mm.	100·63 mm.	103·89 mm.	102·9 mm.
(*GL*) Basi-alveolar	96·12 ,,	94·72 ,,	95·79 ,,	99·02 ,,	105·3 ,,
100 *GL*/*LB*	95·2	95·4	95·2	95·3	102·3

The table shows that this increase is uniform in both measurements so that although the base has considerably lengthened this has not resulted in any prognathism. The figures for the Negro base show that although the modern Egyptian has become longer in the basi-nasal diameter he still remains shorter than the Negro in the basi-alveolar.

This excessive basi-alveolar and basi-nasal length are, I believe, together with certain nasal characters, the most important indications of Negro ancestry.

With reference to the basal measurements, therefore, the cranium of the modern Egyptian suggests negroid admixture, and in this respect also is more primitive than the prehistoric skull.

Facial height and width. In these measurements the modern Egyptian does not appear to have altered to a great extent, but there is a definite diminution in the breadth and slight increase in height, so that the upper face index has increased from 70·6 in the Naqada to 73·8 in the modern Egyptian.

Nasal height and width. The nasal height and width has remained practically constant, but there has been a tendency to an increased smoothness of

the nasal aperture and diminution of the nasal spine. This rounding and smoothing of the lower margin of the nasal opening is a most important Negro feature and its presence in a considerable proportion of modern Egyptian skulls is strongly suggestive of Negro mixture, although there is little tendency to flattening and broadening of the nasal bones or increase in the nasal index.

Females. For comparative purposes I give the means of certain female skulls. The number of these (ten in all) is far too small to be of any value, but even in this number we notice the same change as has been described in the male cranium and this tends to prove the correctness of the male figures.

Females

	Prehistoric Egyptians	Naqadas	Thebans	Modern Egyptians
Height	128·33 mm.	129·47 mm.	130·51 mm.	132·14 mm.
LB	97·64 „	94·86 „	95·29 „	99·75 „
GL	93·69 „	91·02 „	91·93 „	95·62 „
Gnathic index 100 *GL*/*LB*	95·9	95·2	96·5	95·85
Nasal index	50·14	52·3	50·2	52·1

As in the male there is a steady rise in the height of the skull from prehistoric times, associated with an increase in the basi-nasal and basi-alveolar lengths without increase in prognathism.

In the gnathic index, as in the nasal index, the female has a higher figure than the male, falling into line with the general tendency of the female to show more primitive features than the male.

COMPARISON WITH EUROPEAN AND NEGRO SKULLS

Let us now compare the modern Egyptian cranium with the Negro, taking Fawcett's figures (*loc. cit.*) for the latter and with the Whitechapel English of Macdonell (*Biometrika*, vol. III, p. 208).

	Modern Negro	Modern Egyptian	English
L	182·85 mm.	184·5 mm.	189·06 mm.
B	133·15 „	132·56 „	140·67 „
B'	95·91 „	93·65 „	98·02 „
H	135·31 „	137·09 „	132·04 „
OH	115·04 „	118·8* „	114·59 „
LB	102·96 „	103·89 „	101·60 „
GL	105·33 „	99·02 „	95·93 „
GH	68·00 „	69·03 „	70·17 „
GB	96·63 „	93·53 „	90·87 „
NH	49·52 „	50·64 „	51·22 „
NB	27·29 „	25·10 „	24·29 „
100 *B*/*L*	72·87	71·84	74·34
100 *H*/*L*	74·15	74·29	69·97
100 *H*/*B*	101·75	103·3	94·31
100 *B*/*H*	98·28	96·7	106·26
100 *G'H*/*GB* (Facial index)	70·37	73·8	76·5
100 *NB*/*NH* (Nasal index)	55·43	49·57	47·55
100 *LB*/*GL* (Gnathic index)	102·3	95·31	94·4
100 *L*/*LB* (Balance index)	177·6	177·6	186·1

* *OH* on 21 only, of which $H = 140$ mm. Had the whole series been measured the auricular height would be reduced to approximately 116–116·5 mm.

From this it will be observed that in nearly every measurement and index the Egyptian stands in an intermediate position between the European and the Negro, with the exception of the height and length of base, in which he is greater than either, and in the breadth of skull and forehead, in which he is less. If the basal length is taken as a proportion of the maximum length of the skull we obtain the following index $100\,L/LB$ in the three races:

Negro	Egyptian	English
177·6	177·6	186·1

in which the higher figure for the European skull indicates a less proportion of length in front of the foramen magnum.

This is a most suggestive index, for with the assumption of the erect attitude in man there must have been a distinct change in the proportion of skull before and behind this foramen to enable the head to be balanced on the spine. A high index therefore indicates a primitive condition of balance and in this the Egyptian and the Negro appear to have attained the same evolutionary level.

It will be observed that in the characters of length, breadth, height and basal length the modern Egyptian stands in a much closer relationship to the Negro than he does to the European and in most of the indices this position is maintained. In the nasal and gnathic indices, however, which are no doubt the indices in which Negro characters are most pronounced, the Egyptian is distinctly nearer to the European.

DISCUSSION

From the above considerations we are justified, I think, in suggesting that the modern Egyptian skull has certain individual characters which differentiate it readily from European and Negro skulls.

Racially it stands much closer to the Negro than to the European.

It is almost identical in most of its measurements with the crania of prehistoric Egyptians, but has changed along certain lines tending to an increase in height and increase in the length of the cranial base.

These changes may be the result of evolution but it appears more reasonable to suggest that they are the result of racial admixture.

If the objection is raised that changes due to racial admixture should have altered the skull in other dimensions, I suggest that it is only primitive features which are retained from the new race and that all other features are absorbed and eliminated.

This reversion to type or elimination of foreign characters appears to be much more universal than is supposed. Macdonell, in his memoir on the English Whitechapel crania, observed that the crania in question were not Anglo-Saxon or similar to any continental race, but were much closer to the ancient English Longbarrow crania. It is probable that in every case there is a tendency to keep certain racial characters in spite of foreign admixture. Such

admixture with a foreign race may produce a temporary change in the characters of the skull, but there is every reason to believe that unless the supply of the foreign element is constantly kept up reversion to type will occur. This phenomenon is perfectly well known in the breeding of the lower animals and is especially marked with regard to pigeon-breeding, where reversion to the primitive blue rock invariably occurs.

For the purpose of comparing modern Egyptian skulls with prehistoric skulls I have used the Naqada and Theban crania to represent intermediate series. I have done this because these two series are the only complete series of measurements that are easily accessible.

They serve their purpose in indicating the great difference between the dynastic crania on the one hand, and the prehistoric and modern crania on the other.

The Naqada crania were originally supposed to be predynastic, and Fawcett claims that they are about 8000 years old. This is very doubtful and they probably represent a mixture of late predynastic and early dynastic crania. If we turn to Elliott Smith and Derry's figures in *Bulletin No.* 6 (Geological Survey of Nubia) we obtain figures which are undoubtedly correct for predynastic and dynastic crania.

These figures may be compared with my modern series as follows:

	Early predynastic Upper Egypt	4th–6th Dynasty Lower Egypt	Modern Egyptians
L	184·2 mm.	184·0 mm.	184·5 mm.
B	132·0 „	139·1 „	132·6 „
H	132·9 „	136·3 „	137·1 „
LB	100·5 „	102·1 „	103·9 „
GL	97·8 „	96·6 „	99·0 „

This again brings out the difference between the predynastic and dynastic crania and the close similarity between the predynastic and modern crania, with the addition in the latter of increased height and increased cranial base to which attention has already been directed.

A word of warning is due with reference to the so-called prehistoric or predynastic crania. This term has been applied to a primitive type of cranium which is assumed to have existed before the dynastic period.

There is, however, no authority for the assumption that the predynastic type ceased to exist during the dynastic period or that the predynastic people were the progenitors of the dynastic type.

The anthropological evidence is all in favour of the existence of two separate and distinct peoples who, in all probability, lived side by side or who, at least, cannot be differentiated into any time periods. Undoubtedly in dynastic times the different types of culture enable the archaeologist to fix the period with a considerable degree of accuracy, but with the more primitive predynastic people there was little evolution of culture and little to indicate the particular period in which they lived.

It cannot be suggested that the dynastic cranium was evolved from the prehistoric and we are driven to the conclusion that the dynastic people had little or nothing in common with the aboriginal or prehistoric Egyptians.

The pyramid builders and founders of the great dynasties who elevated Egypt to the great state she became were no doubt foreigners who ruled the country and mixed but little with the local people. When the supply of these foreigners diminished and their descendants mixed with the Egyptians there was a gradual deterioration and reversion to the primitive type. Even before the Christian era, the process of elimination of foreign characters was actively progressing and this elimination has continued until all characters of later evolutionary origin have disappeared. The prehistoric Egyptian is the prototype of the fellah of to-day with the difference that the modern denizen of the Nile valley has acquired certain additional characters of a more or less primitive nature from his mixture with the various races who have from time to time ruled him.

I have to express my thanks to my colleague Prof. Derry for his help and criticism during the preparation of this paper.

Adult Male Egyptian Crania

No.	*L*	*B*	*H*	*OH'*	*B'*	*LB*	*GL*	*GB*	*G'H*	*NH*	*NB*
	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.	mm.
1	184·2	136·5	144	120	100	110	101	99·5	73	53·2	27·5
2	185·5	123	140	113	92	110	110	96	71	51	24
3	186	132	143	116·5	86	102	98·5	91	73	53	24·5
4	207	131	145	127	100	110·5	107	95·5	77	52	28
5	180	135	142·5	119·5	95	102	100·5	89	67	52	25
6	186	137·5	139·5	123	95	104	95	89	61	45·5	26·5
7	193	128	147	119·5	90	111·5	104	94	73	48	27
8	182	132	134·5	119·5	90	105	93·5	90	71	54	26
9	180	131	140·5	113·5	94·5	99	100·5	111	66	47·8	27
10	183	136	130	110·5	98·5	103·5	90	100	67	50	27
11	193	137	142	125·5	103	108·5	106	101	73	57·5	27
12	190	134	143	120	87	102	103	92	72·5	52·5	23·5
13	175·5	139	142	122·5	91	100	91	90	72	51	22
14	173·5	139	143	120	98	99·5	94	102·5	63	48	25
15	193	132	136	120	95	108	105	94·5	73	56	27·5
16	198	142	148	126	92·5	108	105	96	70	49	25·5
17	184·5	132	138	117	94·5	103·5	99	—	71	50	25
18	186	132	141	119·5	97	104	98·5	99	64·5	50	25
19	189	130	127	111	97·5	101	103	—	68	53·5	27
20	188	139	143·5	121	—	109·5	103	—	72	52	27
21	191	137	135·5	110·5	93	111·5	104·5	97	72	54·5	27
22	181	131	141	—	93·5	100·5	95·2	96	67	54	24·5
23	174·5	140	131	—	96	103·5	109	—	66	44·4	25
24	186·5	137	139	—	97·5	106·2	100·5	91·5	78	51·2	24
25	178	136	139	—	100	102	98	94	70	51	25
26	180	137·5	132	—	91·5	102·5	98·5	99	66	50	24·5
27	185	127·5	138	—	89	105	98·5	98	63	48·5	24·5
28	180	130·5	131	—	91·5	100	93	82	65	47	24
29	194·5	136·5	141	—	70	110	103	96	95·5	54·5	26·5
30	186	125	134	—	99	101	98	95	70·5	51	27
31	191	138	143	—	97	107·5	110	98·5	72·5	53	27·5
32	190	129	139	—	95	110·2	109·5	96·5	64	49	25
33	187	139	142	—	99	107	97·5	93	67	47·3	26
34	190	139	142	—	98	105·5	95·5	94	73·3	56·5	27
35	187·5	125	129·5	—	93·5	102	103	89·5	70	48	22·5
36	177·5	135	131	—	96	100	101	98	66	46	24
37	192	133	141	—	94	104	97	90	63	48·5	26
38	191	131·5	136	—	101	110	104	95·5	76	51·5	24
39	189	131	134·2	—	101·5	103·5	100	97·5	71	55	26
40	183	131	129	—	92	105	94	93	66	49	23
41	192	134	135	—	94	103·5	102	93·5	66·5	50	28
42	186	131	140	—	99	109·5	106	94	71	50	24
43	185	136	145	—	99	106	98	95	71	52	25·5
44	180	133	140	—	99	106	101	89	78	57·5	28
45	190	133	143	—	98	101·5	94·5	93	69	50	25
46	180	129	130	—	95	98	99	88	70	50	29
47	186	130	133	—	90	103	91·5	91·5	68	51	23
48	183	132	132	—	87·5	105	100	92	67·5	48	24·5
49	178	126	134·5	—	90	103	100	90	71	50	24·3
50	175	127	132	—	86	101	89	84	55	45	25
51	179	137	132	—	86	100	93	86	62	48	26
52	175	131	130	—	87	100	97	102	73	52	25
53	184	117	131	—	94	93	93	94·5	61	47	25
54	173	126	131	—	85·5	103	93	83·2	67	48·3	26·4
55	183	128	135	—	92·5	104	98	92·4	74·2	57·3	25·5
56	178·2	130	131	—	89	97	86	86·2	65·5	47·5	21
57	171·5	139	133	—	97	98	93·2	90·4	73	51·2	23·6
58	172	123·2	125	—	85	96	92	82	61·3	46·5	25

OBSERVATIONS ON THE SUPERFICIAL VENOUS SYSTEM OF THE LOWER EXTREMITY

By CHARLES KOSINSKI

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THE common liability of the superficial venous system of the lower extremity to varicosis has naturally attracted the attention of investigators and a great many memoirs have been written on this subject from the anatomical, physiological and pathological points of view. Among the more important anatomical studies I might mention the memoir by Giacomini (10) who investigated 51 limbs. His anatomical conclusions agree in general with my own: I shall refer to them in detail later. Bardeleben (3), Delbet (8), Klotz (17) and Rima (24) paid particular attention to the valves of these veins. Klotz regarded insufficiency of the valves as the main cause of the varicose condition. This opinion, however, was based on a study of 11 limbs only. Le Dentu (9) investigated the anastomoses between the superficial and deep veins. Houzé (12) contributed a detailed account of the position of and intervals between the valves. Nicholson (22) has recorded the interesting observation that the valves near the termination of the great saphenous are usually healthy even in varicosis.

Despite the many investigations there is no unanimity of opinion about the causation of varicose veins, nor, amongst surgeons and pathologists, a real appreciation of the anatomical facts.

Although attention has been mainly directed to the great saphenous vein for the elucidation of the causation of the varicose condition, the study of the small saphenous vein, which phylogenetically is the more important vein, throws a clearer light upon the problem.

The predisposing cause of varicosis must be the pressure of the long column of blood in the great saphenous vein and the lack of muscular support such as the deeper veins receive. Despite this general predisposition however, varicosis occurs infrequently and then usually in healthy adult people between 20 and 40 years of age (Bergmann (2)).

Several writers state that to a certain extent there is an hereditary tendency to the disease, and according to Magnus in one-half to three-fourths of the cases.

The object of this note is to show that this hereditary factor may be expressed in the modes of arrangement of the superficial veins.

METHOD AND MATERIAL

Altogether I examined 124 legs, of which 70 were males and 54 females, and 66 right and 58 left. In several cases the dissection was facilitated by the use of an injection mass of Berlin blue and gelatine.

I directed particular attention to the following points:

I. The *anatomy* of the small saphenous vein and the relations of its *terminations.*

II. The definite anatomical *anastomoses* of the great saphenous vein with the deep veins of the leg.

I. *Small Saphenous Vein.*

(*a*) It *begins* behind the lateral malleolus where it receives the veins from the lateral portion of the dorsum of the foot, lateral malleolus, and the lateral side and back of the heel. These veins join together to form the small saphenous on an average 2 cm. above the tip of the lateral malleolus. In 20 per cent. this junction was symmetrical in the right and left limbs.

(*b*) The average *diameter* of the vein was 3 mm., the range being from 1 mm. to 4 mm. In 28 per cent. of cases there existed a difference of diameter between the upper and lower half of the vein, and in most of these cases (21 of the 28) the diameter was greater in the lower part. The diminution was from $\frac{1}{2}$ to $1\frac{1}{2}$ mm. and was due to the presence of anastomoses between the small and the great saphenous veins in the middle of the leg. In one-third this difference was present on both sides of the same body.

(*c*) *Its relations to the fascia of the leg.* A great difference of opinion concerning this subject exists. Some writers (Sappey, Hovelacque, Chrétien) claim that it runs under the deep fascia in the upper half; others (Cruveilhier, Malgaigne, Gegenbaur, Gray) that it runs between the superficial and the deep fascia; and others again that it runs between the layers of the superficial fascia (Richet, Tillaux, Cunningham). In the opinion of Spalteholz it runs in the deep fascia, in the so-called "canal aponevrotique" of French authors.

In the great majority of cases (75 per cent.) I found that the vein pierced layers of the superficial fascia to gain the interval between the superficial and deep fascia. The point of piercing was, on an average, in the middle of the leg, the range being from 20 to 75 per cent. of the length of the leg. Only in one-fourth of the cases did it pierce the deep fascia also in the upper third of the leg. Occasionally it coursed between the layers of the superficial fascia on the whole length of the leg. In two cases the vein ran between the superficial and the deep layers in the whole of its course and in three cases it was superficial even to the superficial fascia running just under the skin.

(*d*) Its *relations to the medial sural nerve.* In the majority of cases these relations are extremely variable. In more than half (66 per cent.) of the cases the vein is directly superficial to the nerve in the upper third of the leg; in the middle of the calf it is medial and in the distal third it is lateral to the nerve.

In about one-third of the cases (30 per cent.) the vein is altogether on the

medial side of the nerve, and in about 12 per cent. of the cases the vein is on its lateral side.

Nearly always in the upper half of the leg the nerve is separated from the vein by the deep fascia, and very often also by the connective tissue joining the two heads of the gastrocnemial muscle.

The relations between vein and nerve were the same on both legs of the same body in one-third of the subjects examined.

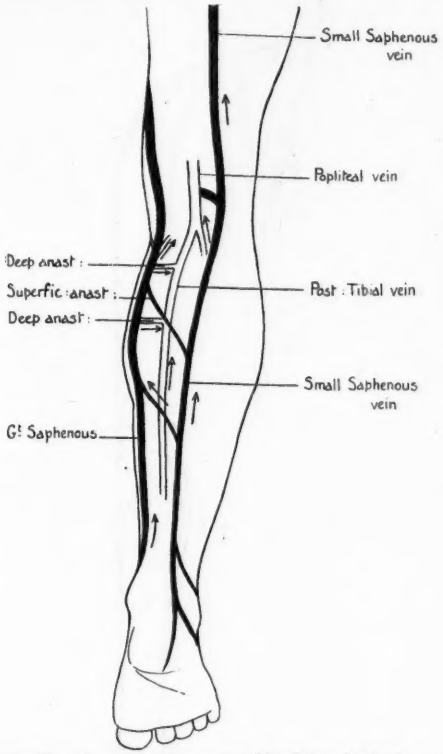

Fig. 1. Small saphenous vein pouring blood into both the popliteal and the great saphenous.

(*e*) ***Relations of the small to the great saphenous and to the deep veins of the leg.*** Usually two to four venous anastomoses join these two superficial vessels, the most constant ones being found in the middle of the leg (figs. 1–3). The main anastomotic vessels run from below upward, and from without from the small saphenous vein inward, to the great saphenous. The valves are so arranged that the blood current flows from small saphenous to great saphenous. The injection mass always flows from the small saphenous to the great saphenous. When the direction of the injection mass is altered (i.e. injected from above) no

injection mass reaches the small saphenous even by great pressure. On the other hand, it is easy to distend the great saphenous vein when the injected mass starts from the small saphenous.

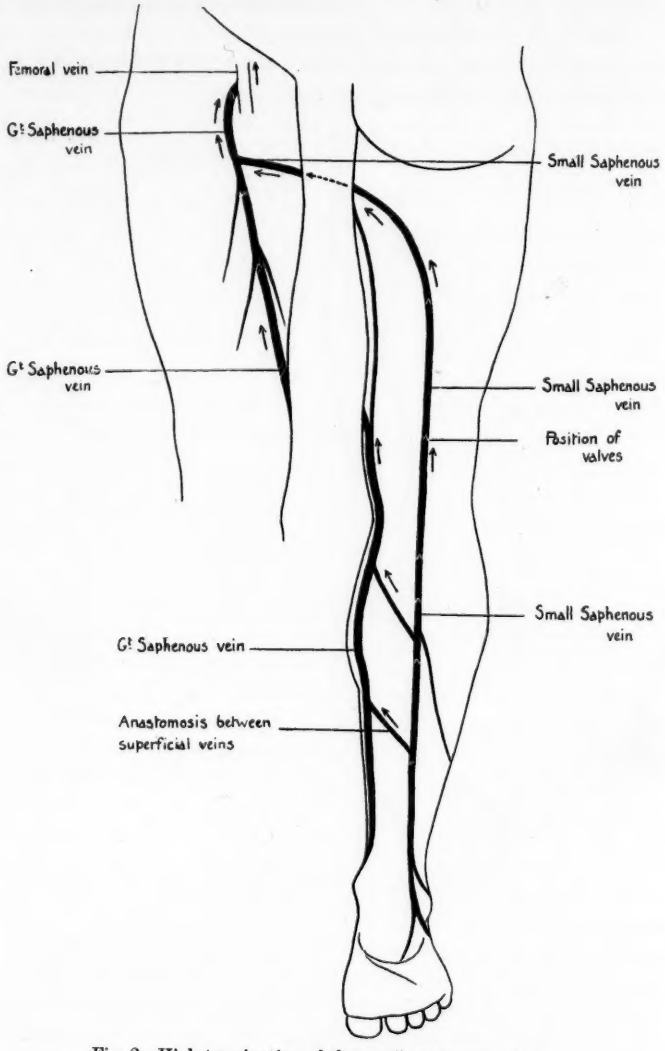

Fig. 2. High termination of the small saphenous vein.

It is therefore important to regard the great saphenous vein in man as the main superficial channel for the venous blood of the lower extremity.

As regards the anastomoses of the small saphenous vein with the deep

venous trunks of the leg, they are extremely scanty and only develop when the small saphenous vein terminates on the leg (about 10 per cent.), not reaching the popliteal space (fig. 3). This anastomosis when present is found in the lower half of the leg, and connects the small saphenous with the venae comitantes of the peroneal artery, the anastomotic channel passing close to the fibula. The usual arrangement is that the deep anastomoses of the great saphenous serve both great and small saphenous veins.

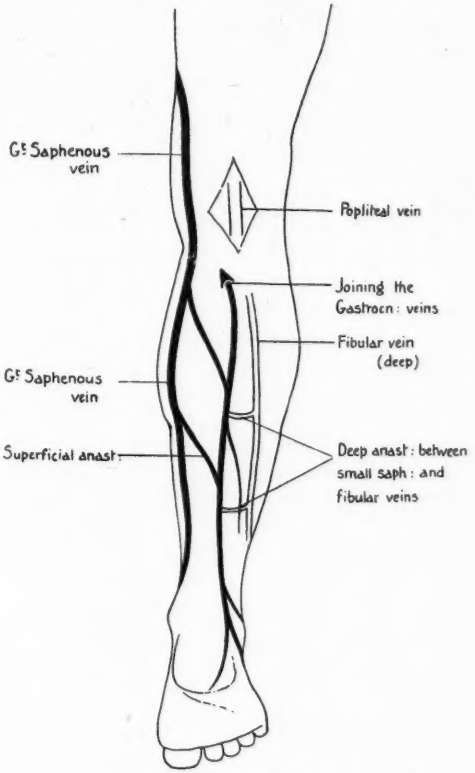

Fig. 3. Low termination of the small saphenous vein.

(*f*) *The number and arrangement of the valves* of the small saphenous vein depend on and correspond to the number of afferent tributaries and in general vary from 4 to 13. The average number is 8. This agrees pretty well with other observers (Houzé, Hovelacque, Cunningham).

Perhaps it would be interesting to consider the number of valves in regard to age and sex. The following two tables summarise the relations:

Table I. *The number of valves in the small saphenous vein in the leg at various ages*

Number of valves	4	5	6	7	8	9	10	11	12	13	Total number of cases
Age 18–29	1	1	3	4	5	4	2	2	—	—	22
30–40	—	2	1	3	2	2	1	2	1	—	14
41–50	—	—	1	3	3	1	—	3	1	1	13
51–60	—	—	2	1	7	1	—	3	—	—	14
61–70	—	1	2	2	7	4	—	2	—	—	18
71–88	—	—	—	—	1	—	1	1	—	1	4
Number of cases	1	4	9	13	25	12	4	13	2	2	85

It follows from this table that in 60 per cent. of cases the number of valves is between 7 and 11, and that this number is independent of the age of the subject.

Table II. *The relation of sex to the number of valves in the small saphenous vein of the leg*

The number of valves	Males	Females	Total
4	1	—	1
5	2	2	4
6	6	3	9
7	8	5	13
8	12	13	25
9	9	3	12
10	3	1	4
11	7	6	13
12	2	—	2
13	2	—	2

The tables show that sex and age have no influence on the number of valves. We see that in one case, aged 28, the number of valves is only 4, and in an old man, aged 88, the number even reaches 13. It is true that with age some valves are slightly degenerated and the walls of the veins are thickened.

The distance between the particular valves varies greatly—from $\frac{1}{2}$ or $\frac{3}{4}$ cm. to 10–12 cm., and occasionally even 15 cm. The average distance is 4·4 cm. (according to Houzé, 4 cm.); the most frequent distance is 2 cm. to 5 cm.

As examples of the usual arrangement of the valves on the leg we give the following formula (going from below upwards), showing the intervals between valves in cm.:

$$5 : 10 : 4 : 2 : 5 : 10 : 5.$$
$$3 : 5 : 5 : 2\tfrac{1}{2} : 4 : 5 : 6 : 10 : 6 : 1.$$

The valves are without exception bicuspid and are situated just below the junction of the tributaries.

(*g*) *The modes of ending of the small saphenous vein.* The variability in the terminations can be expressed as follows:

(1) Most frequently (in 57·3 per cent.: 71 cases) the small saphenous vein joins the popliteal vein in the region of the knee-joint.

(2) In 33 per cent. (41 cases) or in one-third of the cases (according to Giacomini—who investigated 51 limbs—in 26 per cent.): the *high* termination

on the thigh, either into posterior deep femoral veins or into great saphenous vein.

(3) In 9·7 per cent. (12 cases): the *low* termination in the leg, not reaching the popliteal region but ending in the great saphenous vein, or in the deep veins of the leg (usually gastrocnemial veins). These variations are quite independent of sex.

Type (1) may be subdivided into two groups:

(i) In this the small saphenous vein ends exclusively in the popliteal vein. Three-fourths of type (1) belong to this group (42 per cent. = 52 cases). The small saphenous vein forms an arch which enters the popliteal vein on an average at 4·5 cm. above the knee-joint, just below the middle of the popliteal space. The beginning of the arch receives the small superficial posterior vein of the thigh (v. cut. fem. post. of Meyer, v. femoro-poplitea of Hyrtl). This vein begins in the upper or middle third of the thigh, and runs under the deep fascia on the medial side of the small sciatic nerve. In addition, this vein often communicates with the deep posterior muscular veins of the thigh. In rare cases (3) it runs round the medial side of the middle of the thigh towards the great saphenous vein. In 10 cases that posterior superficial vein of the thigh is lacking completely.

(ii) Frequency 15·3 per cent. (19 cases). Small saphenous divides into two branches of equal size. One branch joins the popliteal vein and the other continues the course of the small saphenous vein on the thigh, and ascends to join the great saphenous vein (see fig. 1). The junction with the popliteal vein is at the same level as in the previous group (at 4 cm. above the knee-joint), while the junction with the great saphenous vein is on an average 32 cm. above the knee-joint—in the upper third of the thigh. The branch to the great saphenous vein runs first in the middle line of the posterior surface of the thigh (under the deep fascia), and at a level on an average of about 16 cm. above the knee-joint bends obliquely round to the medial side to join the great saphenous vein.

The relation of the arch of the small saphenous vein to the tibial nerve may be of importance since it explains the obstinate pain in the leg when the veins are varicose. The vein is always intimately connected with the nerve, lying either on the lateral (most often—in 54·5 per cent.) or on the medial side (in 40·9 per cent.). According to Giacomini (10) the first relation occurs in 57·5 per cent., and the second in 42·5 per cent. Occasionally the tibial nerve with its sural branch crosses underneath the arch (in 4·6 per cent.).

Type (2). *High termination* of the small saphenous vein either into the deep posterior veins of the thigh or into the great saphenous vein takes place in 33 per cent. of cases (in 41 cases).

Three varieties can be distinguished:

(i) In 13·7 per cent. (17 cases) it passes entirely into the deep posterior veins of the thigh (the lower perforating veins, especially the third, and the sciatic veins). The level of junction—on an average is about 12 cm. above the knee-joint.

We note the close relation in this variety to the great sciatic nerve, the vein being most frequently on its lateral side. This is important, as varicose veins in this situation may press on the nerve and so cause pain (sciatica).

This termination in the majority of cases takes place through the short head of the biceps muscle. In 2 of these cases a small anatomotic vein was found between the small saphenous and popliteal veins at the level of the knee-joint; and in 4 cases a small cutaneous vein draining the posterior aspect of the thigh joined the main trunk before its entry into the deep posterior veins of the thigh.

The valves present in the femoral portion of the small saphenous vein allow blood to pass in an upward direction. According to Hochstetter(13) the terminal femoral portion in that case is the remains of the primitive sciatic vein which usually disappears.

(ii) In 6·4 per cent. (8 cases), according to Giacomini in 6 per cent. the small saphenous vein divides at the level of the middle of the popliteal space into two branches of nearly equal size, of which one passes to the deep posterior veins of the thigh and the other into the great saphenous vein.

The junction with the deep posterior veins takes place on an average 10 cm. above the knee-joint and that with the great saphenous vein at 26 cm. (range 12–36 cm.) above the knee-joint. The first 16 cm. of its course is subfascial and the last 10 cm. subcutaneous.

The first part is straight in its course, accompanying the small sciatic nerve, while the second part is oblique in direction towards its point of entry into great saphenous vein.

(iii) In 12·9 per cent., according to Giacomini, 14 per cent. This variety occurred in 16 cases of which 6 were males and 10 females, and 6 on the left side of the leg and 10 on the right. This condition was symmetrical in half of the cases (see fig. 2).

We see in this type that all the blood carried by the small saphenous vein drains into the great saphenous vein, and the junction takes place on an average of 31 cm. above the knee-joint, i.e. in the upper third of the thigh, the range being from 18–36 cm. In 4 cases the small saphenous vein was connected with the popliteal vein by small twigs in the region of the knee-joint; and in 6 cases at a higher level are found connections between the small saphenous and the inter- or intra-muscular veins of the thigh.

We find that the direction of the small saphenous vein in the thigh is exactly to the course taken by it in variety (ii)—i.e. that the change from a purely vertical to an oblique path takes place about 16 cm. above the knee-joint, i.e. somewhat below the middle of the thigh. The relations to the deep fascia of the thigh are precisely similar. The diameter of the crural and femoral portion in this variety are found to be the same—namely 2–3 mm. Usually the size increases in the uppermost part owing to the many superficial tributaries on the thigh. The few (2–4) but constant valves in the femoral portion of the small saphenous vein allow the blood to flow upwards only. The dis-

tances between the valves in this portion of the vein are in cm.: 7 : 14 : 10 or 14 : 13 : 2.

The femoral portion of the vein was called "ramus anastomoticus" by Cruveilhier and was regarded by this author as a venous anomaly. In recent text-books it is called "accessory saphenous vein."

Type (3) occurred in 9·7 per cent. (12 cases) (see fig. 3). Here the small saphenous vein terminated in other veins below the knee-joint, either in the great saphenous (variety (i)) or in the deep veins of the calf (variety (ii)).

(i) The frequency of this variety occurs in 8·1 per cent. of legs (10 cases). The junction with the great saphenous vein was variable, but generally takes place in the upper half of the leg and only in 2 cases 1 cm. above the knee-joint. In 4 cases a small cutaneous vein found running down from the popliteal space to join the small saphenous may be regarded as the usual upward continuation of the main trunk; while in 6 cases this apparently small continuation of the small saphenous joined some muscular veins about 5 cm. above the knee-joint.

(ii) The frequency here was 1·6 per cent. (2 cases) (fig. 3). It joined the intragastrocnemial veins, either in the upper third or at junction of middle and upper thirds. As above, the small cutaneous vein passed in a downward direction to join the small saphenous.

To elucidate the varieties described above, the following table is appended:

Type	Variety i %	Variety ii %	Variety iii %	%	Total cases
1	42·0	15·3	—	57·3	71
2	13·7	6·4	12·9	33·0	41
3	8·1	1·6	—	9·7	12

In one-third of cases the small saphenous vein joins directly the great saphenous vein. In two-thirds of cases it joins the deep veins of the lower extremity, either in the popliteal region (most often) or in the thigh or occasionally on the leg. It is very important to note that in 12·9 per cent. of cases (according to Giacomini in 14 per cent.) the small saphenous vein is entirely drained into the great saphenous vein in the upper third of the thigh without any other important connections.

These cases in which the small saphenous vein joins the great saphenous vein, and in 13 per cent. cases this is the main mode of termination of the small saphenous vein, have a direct bearing on the production of varicosity, for there accumulates in the great saphenous vein all the superficial venous drainage of the lower extremity and hence the superficial veins must sustain an increased pressure.

That portion of the small saphenous vein passing into the great saphenous vein in the thigh has only 2–3–4 valves. These are bicuspid and so placed that the current of blood must flow from the small to the great saphenous vein.

Furthermore, this vein in its lower half ascends vertically on the posterior surface of the thigh while in the upper half of its course it winds obliquely

round the medial aspect of the thigh to enter the great saphenous vein almost at right angles (see diagram).

II. *Great Saphenous Vein.*

There is a great difference of opinion as to the direction of the blood-current between the superficial and deep veins.

The majority of investigators suggest that the blood flows from the superficial to deep veins (Spalteholz, Braune, Delbet, Homans, Houzé, Le Dentu, Luschka). Henle and Klotz, however, suppose it possible that the blood may flow in either direction. Theile and Twyman believe that the current flows from the deep to the superficial veins.

I think that the following experiments show that the arrangement of the superficial vein and its anastomoses with deep veins are designed to avoid an accumulation of blood in the great saphenous vein which is the main superficial venous trunk. When the great saphenous vein was injected from above, all the deep veins of leg and thigh were filled with the injection-mass. Ligation of the popliteal vein did not alter the distribution of the injection. On the other hand, all the superficial veins below the level of the main anastomotic channel contain no injected mass.

When the injection is made from below both the superficial and deep veins were filled.

The arrangement of anastomotic channels are by transverse vessels situated:

(*a*) Just below the knee-joint, two or three in number, connecting with the inferior medial articular, superior genicular and intra-articular.

(*b*) At the junction of the middle and superior thirds of the leg—usually two in number, connecting the small saphenous vein with both the medial gastrocnemial and posterior tibial. This latter is the most important channel; it is large enough, the usual diameter being 1½–2 mm., to convey all the superficial blood to the deep vessels, and its course is close to the tibia through the muscular attachments (fig. 1).

(*c*) At the junction of the middle and distal thirds of the leg. This vessel is small and connected to the posterior tibial vein.

(*d*) The anastomoses between the great saphenous vein and the deep veins on the thigh are scarce and usually in the middle of the thigh.

DISCUSSION

As the result of the anatomical investigation of the distribution of the veins and the direction of the flow of injected mass, I can confirm absolutely the experimental conclusions of Luschka, Giacomini, Ledderhose and others that the current of the blood flows from the superficial to the deep veins. Magnus found experimentally that 90 per cent. of injected fluid flowed by way of the deep veins and only 10 per cent. by way of the great saphenous vein. It is noteworthy that the calibre of the great saphenous vein is often less at its termination than in the lower part of the leg.

In every case it has been shown that after ligation of the femoral vein the

main return takes place not by the superficial veins but by the way of intramuscular veins and alongside the great sciatic nerve, eventually to the internal iliac vein (Trzebinski, Karpinski, Müller). From the point of view of development and comparative anatomy this return along the sciatic region is interesting.

From embryology we know that the small saphenous vein represents the post-axial vein of the hind limb bud; it is the first vein to appear and originally opens into the internal iliac through the sciatic and gluteal veins. The subsequent transformation into a short vein opening into the popliteal vein may be an adaptation to the elongation and relative rigidity of the hind limb. This abbreviation of the post-axial vein of the lower extremity is the main difference in the venous system of the fore and hind limbs.

Comparative anatomy seems to indicate that the termination of the small saphenous vein into the popliteal vein is an adaptation peculiar to higher mammals including man.

In animals other than man varicose disease never occurs. They have usually only one superficial vein well developed, namely the small saphenous, the great saphenous being much smaller than it is in man and ending in the lower half of the thigh.

The small saphenous vein in apes and horses ends in the popliteal vein in the region of the knee, while the great saphenous vein ends by joining the femoral vein under cover of the sartorius in the lower half of the thigh. In the horse the posterior vein of the thigh serves to connect the small saphenous vein with the sciatic vein (Chauveau) and is especially well developed in this animal. From the dissections we have made it would appear that in the lower animals the small saphenous ascends to a higher level along the posterior aspect of the thigh.

The factors making for varicosis are:

1. The height of the column of blood. The average length of the great saphenous vein is 85 cm.

2. The thinness of the walls of the vein and the lack of muscular support.

3. The possible variations in the anatomical course of the small saphenous vein and its anastomotic channels.

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NOTE ON THE INNERVATION OF THE VENTRICLE OF THE HUMAN HEART

By ALEXANDER BLACKHALL-MORISON, M.D., F.R.C.P.

The time which usually elapses between the death of man and *post-mortem* examination of his organs, renders the staining of the visceral nerves more difficult in him than in animals from which the parts may be removed immediately after death and prepared for investigation at once.

My general experience, moreover, has been that the younger the animal from which the parts have been removed, the more satisfactory is the result of nerve stains. It was, for example, by staining the nerves in the *pia mater* of the fully developed cat's embryo removed *ex utero*, immediately after the death of the parent animal, that I was able to demonstrate the rich innervation of the intracranial blood-vessels in 1898, which was at that time regarded as non-existent by some authorities (*Edin. Medical Journal*, November, 1898).

The method I employed was one, then, of recent origin, namely Sihler's. It consists in macerating the tissues to be stained in acetic acid, glycerine and a one per cent. solution of chloral hydrate in distilled water, in the proportion of one of each of the two first ingredients and six of the last. Thereafter, in staining the macerated tissue for a week or ten days in a mixture which differs from the first used, only in containing Ehrlich's haematoxylin instead of acetic acid. The stained material is then placed in pure glycerine. Finally, if considered desirable, overstaining may be removed by acetic acid or Pal's solution. Personally, I found that placing the tissues throughout the process in an incubator at a temperature of 100° Fahr. assisted in staining the nerve elements.

The human slide I show is, in accordance with these principles, from the heart of a boy two years old and was treated in the manner mentioned.

The nervous structure displayed is part of the deeper cardiac ventricular innervation. Notwithstanding the many descriptions and delineations to be met with in our own and foreign text-books, it is difficult to determine, in most instances, which of the nerves leaving the cardiac plexuses are vagal and which are sympathetic. The only way to distinguish trunks and branches of the intracardiac vagus from those of the intracardiac sympathetic, is, in my view, the presence of ganglion cells in the former, and this, as we know in the case of the nerves actually in the ventricles, is a rare occurrence. The situation, size, and direction of trunks leaving the auricle for the ventricle, which are more frequently ganglionated, may, however, assist us in this matter. The finer anatomy of the intracardiac nervous system requires investigation by serial sections. The degenerative method, after cutting the nerves, would be most

helpful if successfully practised, but I am not aware that it has even been attempted.

I shall offer some argument in support of my belief, from the character and situation of the human nerves shown, that they are vagal, and shall exhibit a specimen from the sheep showing a nerve definitely distributed to the ventricular muscle, which may, with confidence, be regarded as a branch of the vagus.

The main trunk in the human ventricular nerve shown enters the myocardium of that chamber behind the aorta immediately below the orifice of the right coronary artery, around which may be observed many large and small trunks of the same character. Not in this slide, but in others, I have found nerves round the coronary arteries to hold ganglion cells and Gaskell came to the conclusion on physiological grounds, that all intracardiac ganglia were on the vagal stream. He writes, "the conclusion may be definitely drawn, that all nerve cells in the heart belong to the vagus group and none to the sympathetic" (*The Involuntary Nervous System*, London, 1916, p. 79).

Knowing the difficulty of staining nerves in the human heart, the specimens shown were mounted without any decolorisation of the deep haematoxylin stain, which, if it obscures some details, has the advantage of showing finer ultimate innervation, than would otherwise have been possible in this case.

Unlike man, in whom the innervation of the bundle appears to be derived from a more distant source, in ungulates, as I demonstrated before the Anatomical Society in 1912, the chief avenue for the deeper nerves from the auricular to the ventricular heart, seems to be by way of the auriculo-ventricular bundle and its immediate vicinity. I have placed a specimen from the pig under the microscope stained by Sihler's method, to illustrate this point. It is interesting and indisputable that the most marked effects of experimental block by cutting the bundle are met with in ungulates (Trendelenburg and Cohn, *Archiv. f. d. Ges. Physiologie*, 1910, p. 1). That the chief vagal outflow from the cardiac plexuses to the ventricles, moreover, lies in more or less proximity to the auriculo-ventricular bundle, is also argued from the fact, that, while stimulation of the vagus after clamping this region fails to induce inhibition of the ventricles, the accelerant effect on these chambers of stimulation of the sympathetic persists (Erlanger, *Zentralb. f. Phys.* XIX, 1905, p. 9; Hering, *Archiv. f. d. Ges. Phys.* CVIII, 1905).

The anatomical structure and situation of the trunk and branches shown in the human slide exhibited, appear therefore to argue that these belong to the vagus nerve (fig. 1). From their size, it may be concluded that they supply a considerable area of ventricular muscle, and, by a fortunate section, the finer divisions of a portion of them show the dispersion of nucleated nerve chains into the intermuscular textures, and the implantation of contact bulbs in these chains on the muscle cells and fibres.

Round the implanted bulbs there is usually an area of clearer sarcoplasm which, apparently, does not so fully take the stain as the rest of the nervous

Fig. 1. Human heart: (*a*) large nerve and its branches; (*b*) ventricular muscle; (*c*) neural nuclei; (*d*) artery. Obj. $\frac{1}{6}$; oc. 6; tube drawn out.

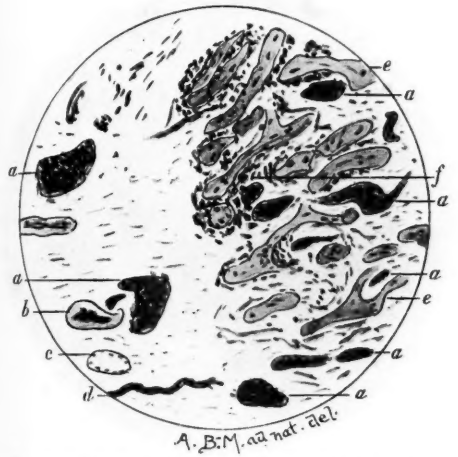

Fig. 3. Auriculo-ventricular bundle in the pig: (*a*) transverse sections of large nerves; (*b*) artery; (*c*) vein; (*d*) small blood-vessel; (*e*) bundle muscle; (*f*) nucleated nerve fibrils. Obj. $\frac{1}{6}$; oc. 6; tube drawn out.

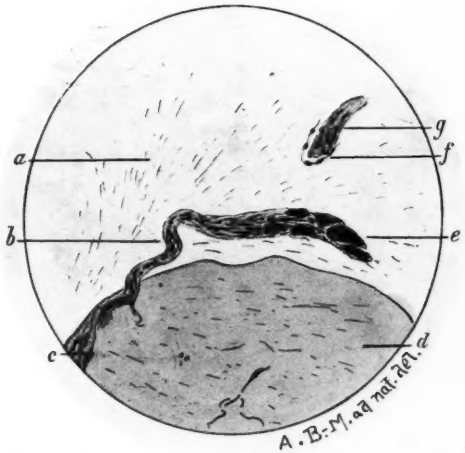

Fig. 2. Sheep's heart: (*a*) connective tissue at the base of the ventricle; (*b*) nerve trunk; (*c*) motor nucleus; (*d*) ventricular muscle; (*e*) ganglion cells in nerve trunk; (*f*) nuclei of the sheath of (*g*) a nerve trunk. Obj. $\frac{1}{6}$; oc. 6; tube drawn out.

structures, because nerve fibrils may be observed in this clearer area and issuing from it. This clearer area resembles what Boeke calls the "sole" with its nuclei and periterminal networks, in his paper on nerve-endings in *Brain* (Vol. XLIV, p. 1 *et seq.*).

It may be that the motor platè, contact bulb or nucleus on ventricular muscle described, is common to both the vagal and sympathetic innervation of these chambers, but, in support of my belief that, in the human specimen shown, the structures are vagal, I have placed under one of the microscopes a specimen from another vertebrate, namely, the sheep (fig. 2) which shows a ganglionated ventricular nerve, and presumably, therefore, in accordance with Gaskell's contention, a vagal nerve, exhibiting a well-defined motor plate or contact nucleus of the same kind, on ventricular muscle. Here also, fibrils emerging from the motor plate may be seen. The contact nuclei, and their respective areas, resemble one another in both animals but are distinguishable one from the other. Such slight differences, however, appear to be constant. Between those of the pig and man, I have found less distinction. Boeke's remarks on this point are of interest: he writes (*Brain*, *loc. cit.*, p. 8), "In every animal the endramification seems to represent a distinct type, so that the motor nerve-endings of a rabbit may be distinguished from those of a hedgehog or bat; and, for instance, the nerve-endings in the muscles of a cow are of a coarser structure than those of the canary. Even in so insignificant a detail as the neuro-fibrillar network, the nerve-ending appears to be in exquisite harmony with its surroundings, a part of the whole, and not a thing in itself."

But there is another mode of nerve termination in ventricular muscle than by the clinging of a nucleated chain to the muscle fibre, namely, that by dichotomous division of fibrils commencing with a triradiate nuclear point of departure of considerable size and followed by others of diminishing proportions. This is manifestly the type of nerve-ending usually found in the sympathetic nerve supply of vessels and textures. I have not yet satisfied myself whether in cardiac muscle, these innervate it alone, or also terminate on vessels and in interstitial tissue. The general distribution to all these structures of these nerve-endings, however, is most probable, as, in the case of the intracranial vessels, I found such terminals could be easily traced to both vessels and pial membrane from the same source (*loc. cit.*).

In view of the discovery of the innervation of striated voluntary muscle by the sympathetic nervous system, the further examination of this point will be of interest in connection with the heart, the only visceral muscle in the mammal having striated fibres, and, like the somatic, also possessed of fibres of varying calibre and marking.

A RARE TYPE OF CONGENITAL CLUB HAND

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Club hand is a deformity which is fairly frequently met with and is due in the majority of cases to defective development of the radial side of the forearm and hand, while only in the minority is it due to abnormality of the ulnar side.

This case was that of a girl aged twenty-one years, who was admitted to hospital suffering from mild Graves' Disease and who had this defect on the ulnar side, associated with syndactylism and partial ectrodactylism.

Her left arm, fig. 1, is normal as far as the elbow but beyond this the forearm is markedly shortened and bowed outwards—while the hand is represented by two fingers fused together, but with separate nails, the smaller one being on the outer side.

Her other hand and her feet are normal.

The X-ray photograph, fig. 2, shows that there is arrested development of the ulna with absence of the lower half.

The radius is bowed outwards and at the elbow does not articulate properly either with the humerus or ulna.

The carpus consists of three bones; the outer or radial one probably represents the trapezium or possibly the fused scaphoid and trapezium, the middle one the trapezoid and the inner one the cuneiform.

Two metacarpal bones are present, viz. those of the thumb and index finger.

The phalanges of the thumb are dichotomous, a condition which according to Keith is frequently encountered in the pollex or hallux of cases showing radial or tibial deformities.

The middle phalanx of the index finger had developed athwart the distal part of the thumb, so that the ungual phalanx of the index finger is on the radial side of the dichotomous ungual phalanx of the thumb. This would account for the larger nail in the photograph being on the ulnar side.

The parents of this patient are not related and there is no history of any developmental abnormality in either of their families, while she has had five brothers all of whom were normal.

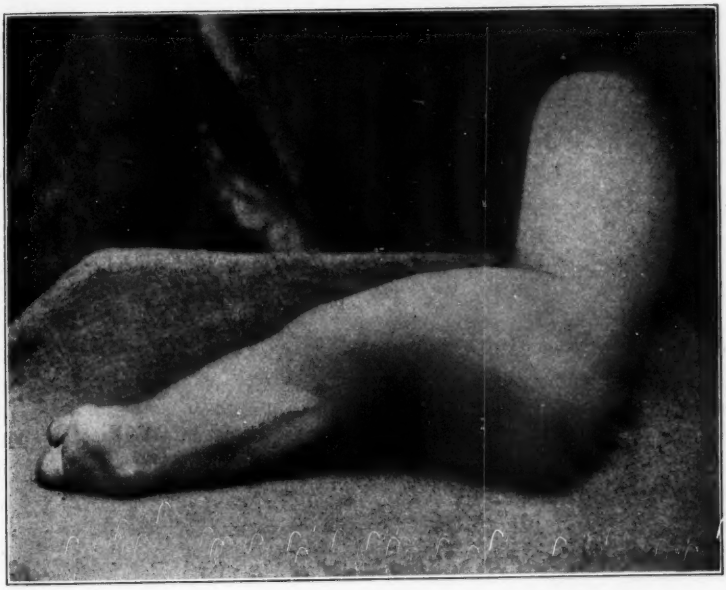

Fig. 1

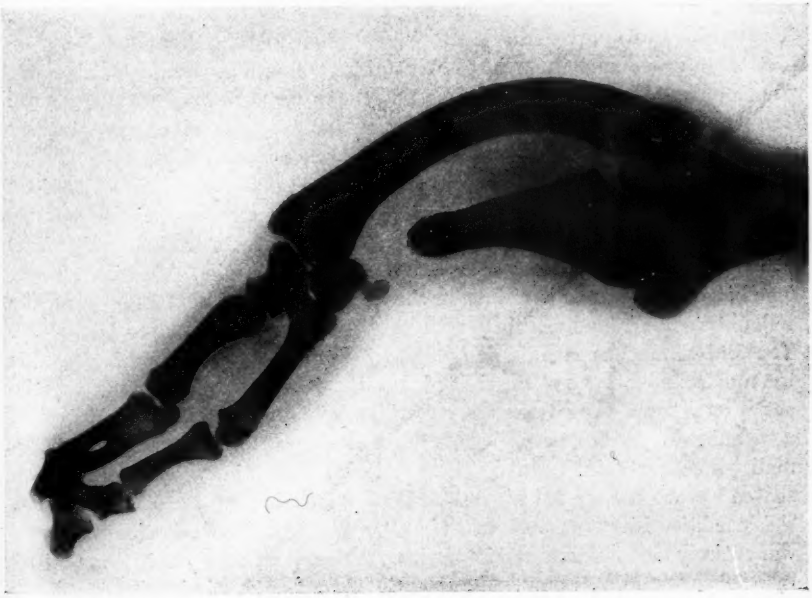

Fig. 2

CONGENITAL ABSENCE OF THE MIDDLE TURBINATE BONE ASSOCIATED WITH PRECOCIOUS OSSIFICATION OF THE LIMB BONES IN A STILLBORN FEMALE

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A PRIMIPAROUS woman with a history of one miscarriage gave birth to a stillborn female child of 7½ lbs. The child presented as a breech with extended legs. Great difficulty was encountered in delivering the breech, the shoulders and the head, which was born chin to pubes. A considerable cephalhaematoma over the left parietal was seen and fractures were felt in the right clavicle and in the neck of the left femur. The radiograms confirmed these fractures and showed centres of ossification of a diameter of 4 mm. in the head of each humerus. The carpus also showed centres of 2 mm. diameter for the os magnum and the unciform. In the lower limb, centres of ossification were present at the lower end of the femur (10 mm.), upper end of the tibia (9 mm.) and in addition to advanced ossification of the os calcis and astragalus, the cuboid presented a centre of 5 mm. diameter. This is the most advanced degree of ossification encountered in the limbs of a series of one hundred stillborn babes. The routine post-mortem displayed no abnormality in the thorax or abdomen, but there was a slight tear in the tentorium cerebelli and some considerable haemorrhage between the tentorium and the upper surface of the cerebellum; the left spheno-parietal sinus was ruptured and an extensive mass of blood clot occupied the subdural space over the left cerebral hemisphere.

The skull, after removal of the brain, was carefully sectioned in the sagittal plane 1 mm. to the right of the mid-line, and the septum was partially removed from the left half of the skull. The left half (fig. 1) presents no abnormality, but the right half (fig. 2) shows complete absence of the middle turbinate bone. The hiatus semilunaris is visible on the right lateral wall of the nose, and the bulla ethmoidalis and unciform process of the ethmoid appear to be normal. The fold of mucous membrane overhanging the hiatus semilunaris (fig. 2) is the mucous membrane of the right side of the nasal septum, left *in situ* by the act of sectioning. The inferior and superior turbinates were normal on this side.

Radiograms of the two halves of the skull showed that there was no abnormality on the left side beyond segmentation of the lamina papyracea as represented by two centres of ossification, the one anterior and the other posterior. This condition is not uncommon at birth. On the right side the lamina papyracea was entirely membranous and its territory was encroached upon to some extent by the surrounding bones. The naso-lachrymal duct, diminutive maxillary

antrum and teeth were normal on each side. The uvula (fig. 1) is bent upwards into the naso-pharynx. This is the normal position in the stillborn.

This case of absence of the middle turbinate is recorded in particular because of the marked difference in the statistics of clinicians and anatomists. The length, breadth and degree of vaulting of the middle turbinate bone are very variable not only from one subject to another, but also from side to side in the same subject. Total absence of the middle turbinate bone is rare in clinical practice, but Zuckerkandl reports this bone as absent in 13 per cent. of a series of 267 sagittal sections of the skull. The middle turbinate bone may be so reduced in size as to be masked by the superior turbinate bone, and for this reason alone one would expect the percentage of cases of absence to be larger in clinical practice than in the dissecting-room.

Comparative anatomy shows that the number of turbinate bones is very variable in monkeys and higher apes, the general tendency being towards a reduction in number to two on each side in the gorilla and orang. Complete absence of all the turbinates has been recorded in three orangs. The reduction in the size of the olfactory parts of the brain as more and more reliance comes to be placed on hearing and sight, as distinct from smell, may have some influence on the number and disposition of the turbinate bones. On the other hand, the huge development of the turbinate bones in carnivores is almost entirely a product of post-natal growth, for during foetal life they display almost human simplicity. This persistence of the foetal character in adult man, as distinct from marked post-natal growth and differentiation as in carnivores, is a typical example of that characteristic to which Bolk has given the name "foetalisation." The adult human nose differs far less from the foetal nose than does the adult carnivore differ from the foetal carnivore. Man retains his adaptable simplicity and leaves specialisation to the losers in the evolutionary race.

The nasal septum, inferior turbinate, and superior turbinate bone do not show such degrees of variation as the middle turbinate bone and Le Double says that he knows of no proven case of absence of the inferior turbinate. The distribution of polypi in the nose is not without a parallel, as polypi are very rarely found on the inferior turbinate or nasal septum but are almost exclusively found on the middle turbinate and in the middle meatus. Thus the bone which is subject to the largest degree of variation up to and including complete absence is also the bone which is most subject to disease, not only as regards polypi, but also as regards those conditions connected with metaplasia of the epithelium such as ozaena. Furthermore, the actual definitive nerve supply of the middle turbinate and its overlying mucous membrane by the nasal branches of the sphenopalatine ganglion of the maxillary division of the trigemenal nerve is subject to considerable variation, and no area of the mucosa displays a higher degree of post-natal growth and differentiation than that of the extensive nasal sinuses. What Sir John Bland Sutton has described as "embryological happenings," together with the marked post-

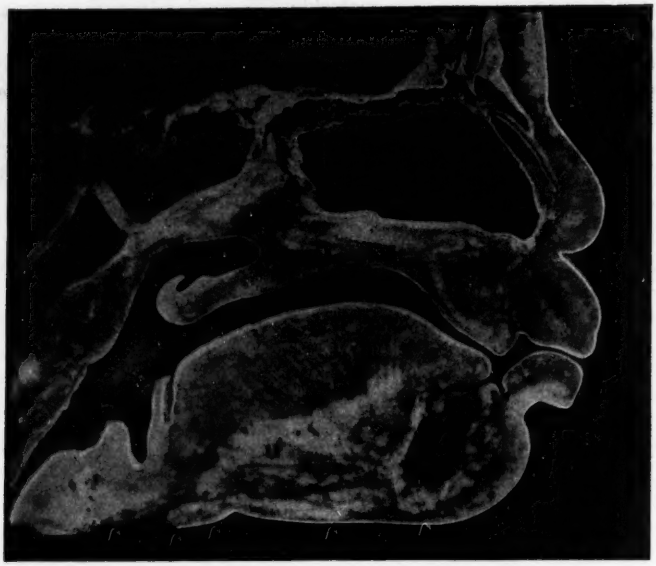

Fig. 1. Left half of skull showing normal conformation of lateral wall of nose and position typical of the uvula in the stillborn.

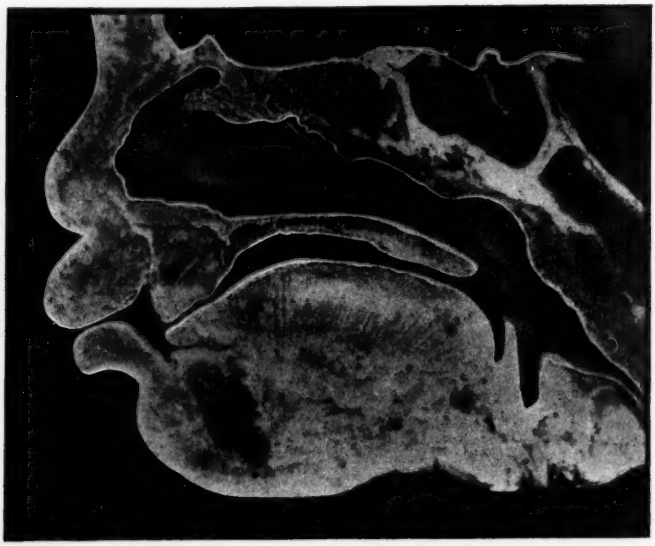

Fig. 2. Right half of skull showing complete absence of the middle turbinate bone leaving the normal hiatus semilunaris exposed.

natal growth and differentiation give to the area of the middle turbinate and middle meatus that vulnerability which Murk Jansen attributes to fast-growing tissues.

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PELVIC AND THIGH MUSCLES OF *ORNITHORHYNCHUS*

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Of recent years attempts to establish homologies between the muscles found in one class of Vertebrates and those in another have been placed on a much sounder basis by the study of the fossil bones of common ancestral forms. These bones often show muscle insertions as well marked as those on the bones of animals living to-day. Moreover, being often intermediate in shape, they indicate how the skeletal differences between living groups have arisen, differences intimately connected with the different position and action of the muscles moving that skeleton. Watson in England, Gregory and Camp in America, were pioneers in this line of work. More recently Romer[1], using similar methods and also considering the nerve supply, has made a very careful comparative study of the locomotor apparatus in Amphibia, Reptiles and Mammals with especial reference to the mammalian line of descent. Of these three classes he himself dissected three living types, *Cryptobranchus*, *Iguana* and *Didelphys*, but at that time no Monotreme, relying on Westling's description of conditions in this group.

Recently I have had the opportunity of dissecting the hind limb musculature of two specimens of *Ornithorhynchus* (kindly lent me for this purpose by Prof. D. M. S. Watson). I find that, in the light of Romer's results from other groups of vertebrates, many of Westling's homologies can no longer be accepted; moreover they are unaccompanied by any figures. Although since the days of Cuvier and Meckel there have been other, partially illustrated, descriptions by Mivart, Alix, Coues, Manners-Smith and Frets, the homologies of these investigators are for the most part equally unacceptable, so that a new and fully illustrated description of these muscles seems to be needed.

I have myself dissected specimens of Romer's three types, and also of other lizards and of the marsupial *Sarcophilus*, and I have had the opportunity of discussing some of the difficult points with Dr Romer himself, convincing myself of the validity of almost all his homologies. Most of the pelvic and thigh muscles of *Ornithorhynchus* can readily be brought into line with these. As might be expected, they are essentially mammalian in their arrangement but sometimes still suggest a reptilian origin. A few appear to be unique.

[1] Romer (1922), "The Locomotor Apparatus of Certain Primitive and Mammal-like Reptiles. *Bull. Am. Mus. Nat. Hist.* XLVI.

I. MUSCLES SEEN WITH THE ANIMAL ON ITS SIDE

"Cruro-coccygeus."

Origin. In front by a few fibres arising from the anterior end of the iliac blade at its internal corner. Then along a short tendinous raphe stretching between this and the spine of the first sacral vertebra superficial to spinalis and semispinalis lumborum. Then along the spines of the first sacral to the fifth caudal vertebrae. Then from the fascia of the tail external to all the tail muscles, and a little way on to the ventral surface of the tail beneath the transverse process of the fifth caudal vertebra (or thereabouts).

Insertion. (*a*) By a wide, flat tendon which passes round the back of the ankle, on to the under surface of the foot internal to the origin of gastrocnemius and (in the male) external to the spine. Here it is superficial to all the tendons of the leg muscles.

(*b*) By a partly fleshy, partly tendinous insertion on to the preaxial border of the tibia, internal to gracilis and just distal to the insertion of semimembranosus and semitendinosus.

This enormous muscle is the hardest of all the monotreme muscles to interpret. I should judge it to be used by the animal in kicking back the earth scraped out from the burrow, and know of nothing that really corresponds to it in any reptile or higher mammal. Against its being part of glutaeus maximus, as it has usually been named (e.g. Manners-Smith[1], Westling[2]), is its insertion; this is on the lower leg, to which it passes superficially to biceps, instead of on the femur internal to biceps. Its mode of insertion would seem rather to relate it to a part of the reptilian flexor mass, the origin of which had not travelled down the ilio-ischiadic (mammalian sacro-ischiadic) ligament to the tuber ischii, as that of the semimembranosus and semitendinosus of most mammals has done. It may be related to the cruro-coccygeus of *Didelphys*, a slender muscle passing from the side of the tail to the lower leg, and represented in various other mammals by slips joining or accompanying semitendinosus or biceps (Romer, p. 573). This, Romer suggests, may further represent the long tendon of the reptilian caudi-femoralis (caudi-femoralis longus). The primitive caudi-femoralis is, as Romer points out, closely associated with the long flexor muscles, inserting into the flexor mass in Urodeles and primitive frogs. Frets[3] calls the anterior part of the disputed muscle in *Ornithorhynchus* glutaeus maximus, the hinder part caudo-femoralis.

Biceps [Reptilian ilio-fibularis; Romer, p. 564].

Origin. From the ischial tuberosity. Passes deep to "cruro-coccygeus" and superficial to all the femoral muscles.

[1] Manners-Smith (1885), "On some points in the Anatomy of *Ornithorhynchus paradoxus*," *Proc. Zool. Soc.*

[2] Westling (1889), "Anatomische Untersuchungen über Echidna," *Bihang k. Svenska Vet.-Akad. Handlingar*, XV.

[3] Frets (1910), "Über den plexus lumbo-sacralis, u.s.w.," *Morphol. Jahrb.* XL.

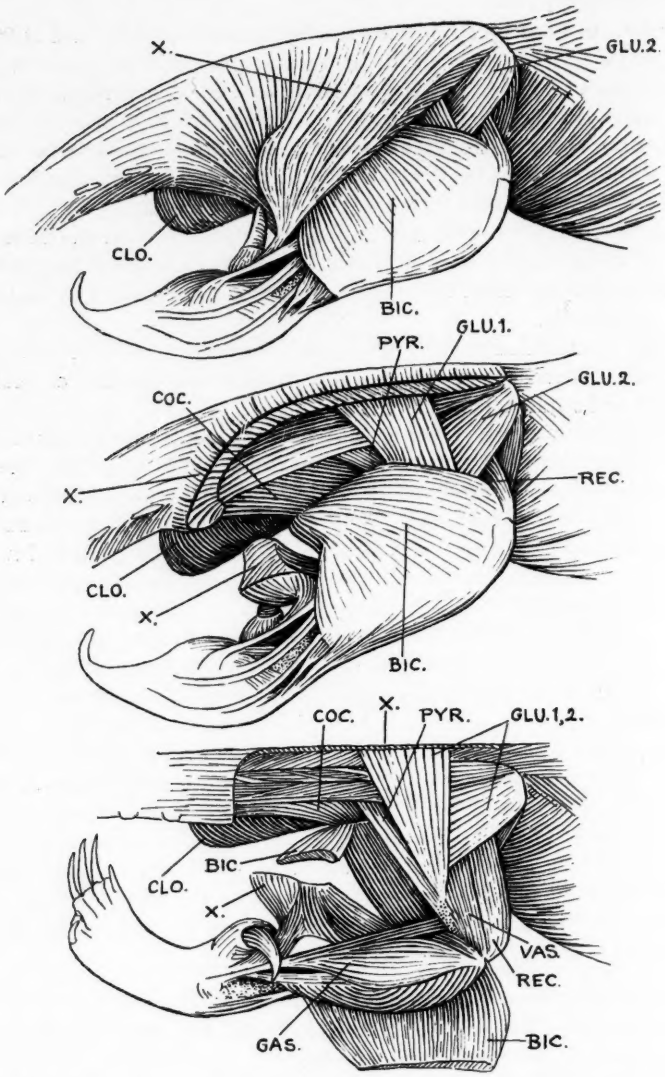

Fig. 1. The right pelvic and thigh muscles of *Ornithorhynchus*, as seen with the animal on its side.

BIC. = biceps; CLO. = cloacal pouch; COC. = ischio-coccygeus; GAS. = gastrocnemius; GLU. 1, 2. = glutaeals; PYR. = pyriformis; REC. = rectus; VAS. = vastus; X. = "cruro-coccygeus."

Insertion. Into the fascia covering the lower leg muscles on the anterior and external surface of the lower leg.

Glutaeals [Reptilian ilio-femoralis; Romer, p. 570].

In *Ornithorhynchus* there are two glutaeal muscles.

(*a*) (= "Glutaeus medius" of Westling and Frets).

Origin. By a thin tendinous margin immediately under the fleshy origin of "cruro-coccygeus."

Passes to the femur superficial to the axial musculature and to the other glutaeal.

Insertion. On the posterior (external) border of the femur at the distal extremity of the crest running down that border from the great trochanter. The area of insertion is small, and distal to the long one of the other glutaeal.

(*b*) (= "Glutaeus minimus" of Westling and Frets).

Origin. From nearly the whole of the glutaeal fossa of the ilium.

Passes backwards and outwards, covering the origins of rectus and vastus.

Insertion. On to the dorsal surface of the great trochanter and the crest running from that trochanter down the posterior (external) border of the femur.

The first of these two glutaeals, (*a*), corresponds most nearly to the Eutherian glutaeus maximus, the second, (*b*), to a fused glutaeus medius and minimus. In neither of my specimens was there any sign of a division of this second glutaeal into two, as described by Manners-Smith.

Pyriformis [Reptilian caudi-ilio-femoralis? Romer, p. 572].

Origin. From the transverse process of the second caudal vertebra just dorsal to the anterior fibres of ischio-coccygeus.

Insertion. On the ventral surface of the femur beyond the obturator insertions, and close to the most distally inserting part of the glutaeus, on the posterior (external) border of the bone.

For this, as for the other muscles from tail to limb, it is hard to find the reptilian equivalent. The American workers have suggested that it is the reptilian caudi-ilio-femoralis (coccygeo-femoralis brevis). This in reptiles "inserts by a tendon into the femur part way down the shaft, reaching the bone between ilio-femoralis and the adductors" (Romer, p. 572). In higher mammals pyriformis inserts on the ventral surface of the great trochanter. The monotreme muscle, although undoubtedly representing the pyriformis of higher forms, has an insertion some way down the shaft of the femur, in the position of the reptilian caudi-ilio-femoralis. This makes the suggested homology a very probable one.

Rectus [= Reptilian caput iliacus triceps or extensor ilio-tibialis; Romer, p. 562].

Origin. From a small area on the ilium immediately in front of the acetabulum. There is a distinct tubercle for it at the acetabular end of the ridge between the glutaeal and iliac fossae of the ilium.

Passes between the glutaeals and ilio-psoas and then superficial to vastus. Its insertion may be taken with that of vastus below.

Vastus [= Caput femoralis triceps or femoro-tibialis; Romer, p. 564].

Origin. From the whole of the dorsal surface of the femur except for the insertion places of the glutaeals and ilio-psoas on the dorsal surfaces of the two trochanters.

The muscle has a thick fleshy body lying between vastus and the femur.

Insertion. Together with rectus on the patella and patella ligament.

Sartorius [= Caput acetab. triceps or Ambiens; Romer, p. 563].

Origin. From the extremity of the ilio-pectineal spine (the long process projecting forwards from the anterior border of the pubis just below the ilio-pubic symphysis).

Insertion. On the front of the knee joint, proximally to and in a line with the insertion of gracilis, and at some little distance beyond the insertion of the adductors.

As pointed out by Romer the sartorius of monotremes, like the ambiens of reptiles, arises from the pubis in front of and a little below the acetabulum, instead of from the superior iliac spine as in most higher mammals. Monotremes are unique, however, in having the anterior border of the pubis in this region drawn out into what I have termed above the ilio-pectineal spine, and it is from the tip of this spine that sartorius takes origin.

II. MUSCLES SEEN WITH THE ANIMAL ON ITS BACK

Gracilis [= Reptilian pubo-ischio-tibialis; Romer, p. 570].

Origin. Mid-ventrally from the whole length of the pelvic symphysis and forwards from here along the median border of the "marsupial" bone for about two-thirds of its length.

Passes superficial to the adductors, completely concealing them.

Insertion. On the anterior border of the tibia just external to the insertion of the adductors and of "cruro-coccygeus." The insertion is a long one, reaching about half way down the tibia from the insertion of sartorius on the knee joint.

Semitendinosus and semimembranosus [= the Reptilian flexor tibialis internus and externus group; Romer, p. 570].

Origin. Along the hinder border of the ischium, between the origin of biceps on the ischial tuberosity and that of gracilis on the pelvic symphysis.

The two muscles are imperfectly separated. They are hidden by gracilis ventrally and by biceps postero-dorsally. Semitendinosus has the more dorsal origin, spreading a little anteriorly to the ischial tuberosity until its area of origin borders on that of the dorsal obturator muscle.

Insertion. Into the strong ridge that runs down the anterior (mesial) border of the tibia. The insertion reaches from that of the adductors at the knee joint,

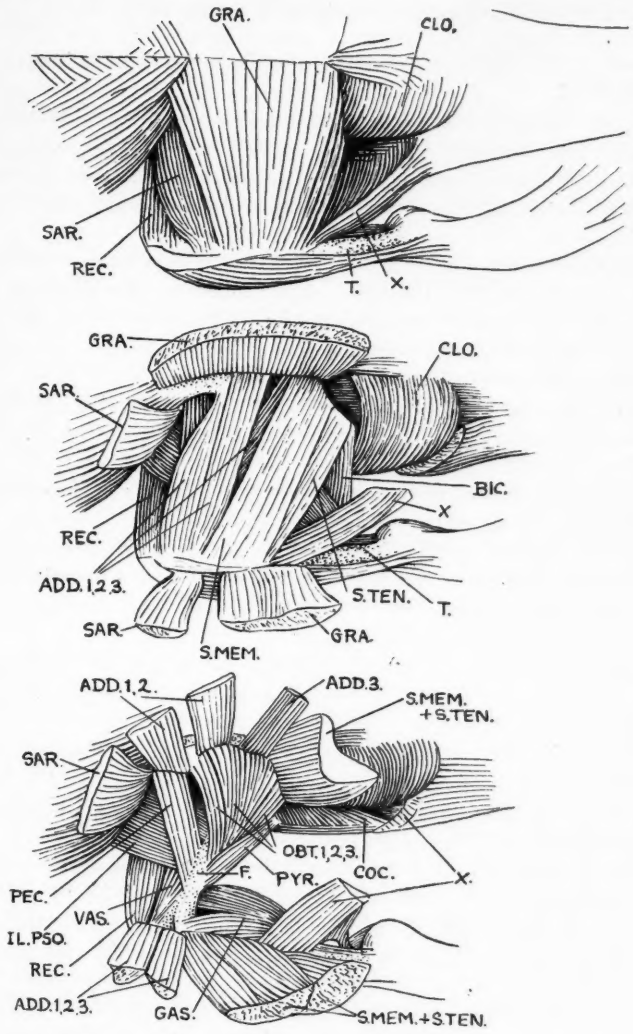

Fig. 2. The right pelvic and thigh muscles of *Ornithorhynchus*, as seen with the animal on its back.

ADD. 1, 2, 3. = adductors; BIC. = biceps; CLO. = cloacal pouch; COC. = ischio-coccygeus; F. = femur; GAS. = gastrocnemius; GRA. = gracilis; IL. PSO. = ilio-psoas; OBT. 1, 2, 3. = obturators (including gemelli, etc.); PEC. = pectineus; PYR. = pyriformis; REC. = rectus; SAR. = sartorius; S.MEM. = semimembranosus; S.TEN. = semitendinosus; T. = tibia; VAS. = vastus; X. = "cruro-coccygeus."

downwards within those of sartorius and gracilis for about one and a half centimetres, where it touches the insertion of "cruro-coccygeus."

Adductors [= Reptilian ischio-femoralis or pubo-ischio-femoralis; Romer, p. 571].

So much confusion exists in the use of the terms "brevis," "longus," "parvus," "magnus," differently applied by different writers to the several mammalian adductors, that I shall not here attempt to distinguish them by any of these names. The adductor mass in *Ornithorhynchus* is divided at its origin into three:

1. The most anterior adductor.

Origin. From the little tubercle ("pubic tubercle") which projects from the pubis just lateral to its articulation with the "marsupial" bone.

This muscle covers the ventral surface of pectineus and inserts together with:

2. The median adductor.

Origin. Along the articulation of the "marsupial" bone with the pubis, and on the anterior border of the pubis just behind this articulation and in front of the origin of obturator externus.

It is covered externally by gracilis, bordered behind by semimembranosus, and in front by the anterior adductor.

Insertion. Together with the anterior adductor on the inner side of the knee, on the medial condyle of the femur, just above the insertion of semimembranosus on the tibia.

3. The posterior adductor.

Origin. Immediately lateral to the pelvic symphysis (which is occupied by gracilis) and near to its posterior end, where it is practically confluent with semimembranosus.

A small muscle, almost entirely concealed by semimembranosus and by the median adductor.

Insertion. Its fibres are lost among those of the median adductor before reaching the knee.

The ischio-femoralis of lizards inserts towards the proximal end of the femur. In higher mammals the adductors usually have a long insertion area on the ventral (posterior) surface of the femur, but more distally than in lizards. This area is left bare in *Ornithorhynchus*, where the adductors insert entirely at the distal end of the femur. In *Echidna*, however, Frets finds that they insert "on the distal third of the median margin and on the tibial condyle." Professor Watson has suggested to me that the condition in *Ornithorhynchus* is associated with the swimming habits of that animal.

Pectineus [= part of Reptilian pubo-ischio-femoralis internus; Romer, p. 565].

Origin. From the anterior border of the girdle between the attachment of the "marsupial" bone and the extremity of the ilio-pectineal spine.

Lies between the more superficial sartorius and the deeper ilio-psoas.

Insertion. About midway along the anterior (median) border of the femur at the distal end of the ridge leading down that border from the lesser trochanter. The area of insertion is sometimes marked by a slight prominence on the femur.

It is probable, as Romer has shown, that most of the reptilian pubo-ischio-femoralis internus has in mammals migrated upwards on to the ilium and lumbar vertebrae as the ilio-psoas, but that the small pectineus represents a portion that has retained almost its original position.

Ilio-psoas [= main part of Reptilian pubo-ischio-femoralis internus; Romer, p. 565].

Psoas and iliacus form practically one continuous mass.

Origin. The ventral surface of the presacral vertebrae from about half way along the animal's back to the sacrum (= psoas minor), from the anterior sacral vertebrae (= psoas major) and from the whole of the iliac fossa of the ilium (= iliacus).

Insertion. The more anterior part representing psoas minor inserts on the ilio-pectineal spine alongside sartorius. The more posterior part (psoas major and iliacus) inserts on the dorsal surface and anterior (median) border of the femur.

This latter area of insertion is a triangular one, reaching from the extremity of the trochanter minor to about half way down the shaft of the femur.

Obturators.

The obturator externus, quadratus femoris, gemelli and obturator internus of higher mammals are represented by the following muscles in *Ornithorhynchus*.

A. A mass which lies beneath the adductors and arises partly from the membrane covering the obturator foramen but chiefly from the bordering parts of the girdle. At its origin this mass is divided into:

(1) The most anterior obturator muscle ("obturator intermedius" of Westling).

Origin. From the pubis anterior to the obturator foramen, between the latter and the base of the marsupial bone. A few fibres may take origin from the membrane covering the foramen itself.

Insertion. Together with (2) described below.

(2) The median obturator ("obturator externus" of Westling).

Origin. From a large area on the ventral part of the ischium and pubis, below and posterior to the obturator foramen, under cover of semimembranosus and gracilis.

Lies immediately over the obturator foramen and some of its fibres may take origin from the membrane covering the latter.

Insertion. Together with the anterior obturator on to a wide area on the ventral surface of the femur at its proximal end. Most of the fibres of the

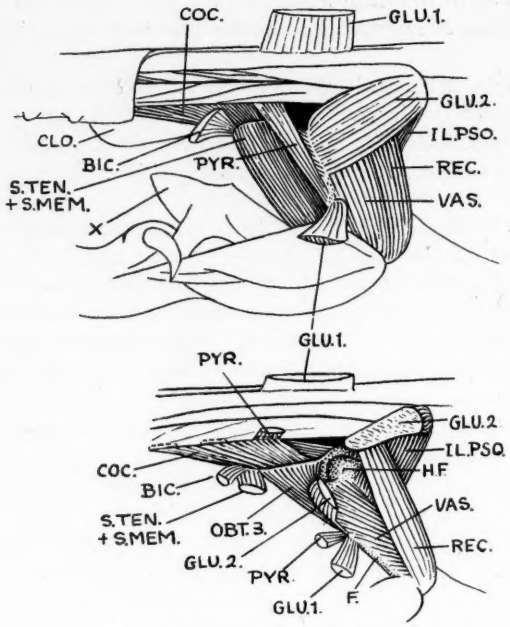

Fig. 3. Deep lateral aspect.
H.F. = head of femur. Other letters as in preceding figures.

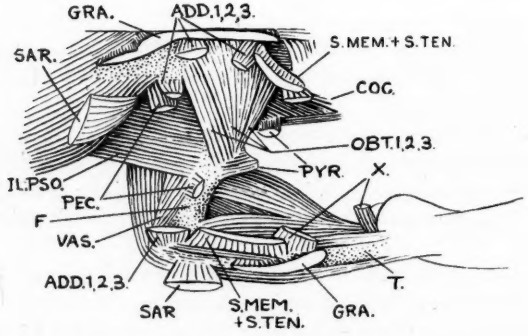

Fig. 4. Deep ventral aspect. Lettering as in fig. 2.

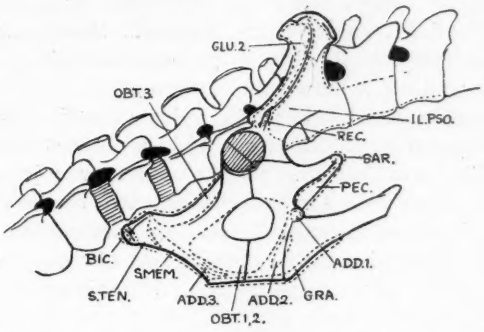

Fig. 5. Pelvis of *Ornithorhynchus* from the right side with muscle areas indicated by dotted lines.
ADD. 1, 2, 3. = adductors; BIC. = biceps; GRA. = gracilis; GLU. 2 = deeper glutaeal (medius + minimus); IL.PSO. = ilio-psoas; OBT. 1, 2. = obturator externus (+ quadratus femoris?); OBT. 3. = ? obturator "internus" + gemelli; PEC. = pectineus; REC. = rectus; SAR. = sartorius; S.MEM. = semimembranosus; S.TEN. = semitendinosus.

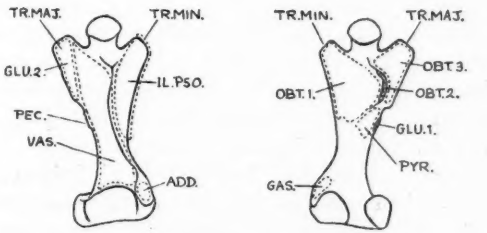

Fig. 6. Dorsal (to the left) and ventral (to the right) aspects of the right femur of *Ornithorhynchus*. Muscle areas indicated by dotted lines.
ADD. = adductors; GAS. = gastrocnemius (internal head); GLU. 1. = glutaeus "maximus"; GLU. 2. = glutaeus "medius + minimus"; IL.PSO. = ilio-psoas; OBT. 1, 2. = obturator externus (+ quadratus femoris?); OBT. 3 = ? obturator "internus" + gemelli; PEC. = pectinus; PYR. = pyriformis; TR.MAJ. = trochanter major; TR.MIN. = trochanter minor; VAS. = vastus.

median obturator, which has large fleshy origin but tapers distally, insert on to a low crest bounding this wide area posteriorly and dividing it from the smaller area of insertion of the "obturator internus" to be described below.

This mass (headed A above) clearly represents the obturator externus of higher mammals and probably also the quadratus femoris.

B. A smaller but nevertheless quite stout muscle.

Origin. Along the dorsal border of the ischium from just behind the acetabulum to the origin of semitendinosus and biceps on the tuber ischii.

Insertion. On the ventral surface of the trochanter major and of the crest passing from the latter down the posterior (external) border of the femur.

This muscle has been variously homologised with obturator internus, the gemelli, quadratus femoris and the superior part of obturator externus. By its insertion it would appear to represent obturator internus and the gemelli of higher mammals. Unlike the latter, *Ornithorhynchus* has no true obturator internus taking origin from the inner surface of the ischium. The muscle just described is completely excluded from that surface by the broad insertion of ischio-coccygeus. Romer (p. 569) wishes to derive the typical obturator internus from the reptilian ischio-trochantericus (pubo-ischio-femoralis posterior), a small muscle arising from within the pelvis posteriorly and passing out over the dorsal border of the ischium to insert into the proximal end of the femur. He shows that in primitive fossil reptiles such as *Diadectes* and *Dimetrodon*, and in some Therapsid (or "mammal-like") reptiles such as *Moschops*, there is a small but well-marked fan-shaped muscle area "just within the dorsal border of the ischium and converging to the representative of the 'lesser sciatic notch'." In other words, he thinks that a femoral muscle arising from within the pelvis posterior to the ilium is far older in origin than the mammals, although in many of these it acquires a new importance, becoming much larger and spreading down within the pelvis over the obturator region.

If this view is correct the monotreme condition cannot be intermediate between primitive reptiles and higher mammals, for the monotremes have either lost the ischio-trochanteric muscle or it has been pushed up on to the dorsal border of the ischium by ischio-coccygeus.

I have elsewhere suggested that the disputed muscle in monotremes might well, both from its origin and from its insertion, represent the postero-dorsal division of the big reptilian pubo-ischio-femoralis externus (the other divisions of which become obturator externus). Yet, except that it does not reach down within the pelvis at its origin, it has undeniably the appearance of an obturator internus muscle[1]. It is therefore possible that the modern placental obturator

[1] It may be noted that even in some marsupials the obturator internus consists of only a few insignificant fibres. Macalister, 1870 and 1872, *Mag. Nat. Hist.* 4th ser. vols. v and x, reports that there is no obturator internus in either *Phascolomys* or *Sarcophilus*. In a *Sarcophilus* which I myself dissected, however, I found a thin slip of muscle arising from well within the pelvis. This became tendinous where it rested on the surface of another muscle ("gemelli") arising from the postero-dorsal border of the pelvis by an origin almost as extended as that in monotremes. The ischio-coccygeus muscle inserted, as in placentals, anterior to the slender obturator internus but not completely anterior to the representative of the gemelli.

internus was not derived from the modern reptilian ischio-trochantericus (in this case an independent and somewhat parallel development), but from a muscle taking origin from the outer surface and dorsal border of the hinder part of the girdle. The gemelli of placentals would represent some fibres of that muscle which did not migrate down within the pelvis. This might help to solve the problem of ischio-coccygeus, which inserts in placentals anterior to obturator internus, permitting its derivation from the reptilian ischio-caudalis, a powerful muscle passing from the tail to the ischial tuberosity and inserting *posterior* to ischio-trochantericus. The monotremes would represent an intermediate condition, for in them ischio-coccygeus has so wide an insertion within the girdle that there is no room for any other muscle to arise there, be its origin that of an ischio-trochantericus or that of an obturator internus. Might not the muscle area in Permian reptiles which Romer ascribes to the origin of an ischio-trochantericus equally well be the insertion of an ischio-caudalis? Certainly in Romer's figures of *Dimetrodon* and *Moschops* it lies in the position of the insertion area of ischio-coccygeus in *Ornithorhynchus*.

Ischio-coccygeus [= all or part of Reptilian ischio-caudalis?].

Origin. From the transverse processes of the second, third, fourth and fifth caudal vertebrae. The fibres arising from the second caudal vertebra are beneath those of pyriformis.

Insertion. On the inner surface of the ischium close to the origin of the dorsal obturator along its dorsal border.

The homologies of this muscle I have just discussed in relation to those of the obturators. If it really represents ischio-caudalis it has become very much shortened, but that is true of all tail muscles in the change from reptile to mammal, when the tail ceases to be of importance in locomotion.

ON CERTAIN FEATURES OF THE ORBITO-ETHMOIDAL REGION IN THE CYCLOSTOMATA, PLAGIOSTOMI AND TELEOSTOMI

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In the three above-mentioned groups of fishes the nasal capsules and nasal apertures, and the ectodermal attachment of the hypophysial pit, or cord, differ markedly in their relations to the snout and to the trabeculae, and it is the purpose of the present paper to attempt an explanation. It will be assumed throughout the discussion, that the trabecular and polar cartilages are, respectively, the pharyngeal elements of the premandibular and mandibular arches, and that the hypophysial pit is a median space left between two curved ectodermal surfaces that have been rolled, hinge-like, one upon the other (Allis, 1923, 1924 *b*). One of these ectodermal surfaces lies external to the ventrally and antero-ventrally presented surfaces of the embryonic brain, and the other to the anterior end of the alimentary canal, and they may be called, respectively, the frontal and visceral arch surfaces.

The conditions in the Selachii will be first considered.

There is, in embryos of *Acanthias*, a pronounced cranio-cerebral flexure, and as a result of this the pharyngo-premandibular (trabecula) of either side is forced downward and backward so that its primarily dorsal end lies slightly below the ventral end of the pharyngo-mandibular (polar cartilage), as is well shown in van Wijhe's (1922) figure of the skull of a 29 mm. embryo of this fish. The pharyngo-mandibular is not affected by this flexure, and still retains its primitive position perpendicular to the notochord. In a 39·5 mm. embryo, these two pharyngeal elements have fused with each other, end to end, and the pharyngo-mandibular has fused, by its dorsal end, with the ventral surface of the parachordal. In embryos of *Pristiurus* and *Scyllium*, similar fusions of these two cartilages also take place (Sewertzoff, 1899 and Goodrich, 1918), and comparison of the skulls of the adults of these three fishes with those of others of the Selachii has led to the justifiable conclusion that similar fusions take place in all of them.

The hypophysial pit of these fishes opens into the stomodaeum slightly anterior to the oral plate (velar membrane, Kerr), and as the upper lip develops anterior to this point (His, 1892, figs. 13–14), the opening of the pit lies in the buccal cavity. From there the pit extends inward to the infundibular region of the brain, and the hypophysis of the adult develops in relation to its deeper portion, the remainder of the pit first becoming closed and the cord, or stalk, so formed then disintegrating and becoming transformed into mesenchyme. The

pharyngo-premandibulars and pharyngo-mandibulars both lie, primarily, wholly in visceral-arch tissues, and morphologically posterior to the tip of the hypophysial pit.

In the adults of these fishes the hypophysis lies in the cranial cavity, and hence dorsal to the trabeculo-polar bars formed by the fusion of the pharyngo-premandibulars and pharyngo-mandibulars. The nasal capsules lie lateral or ventro-lateral to the trabecular plate, formed by the fusion of the trabeculae, and they may even approach each other ventral to that plate and there meet and fuse, thus forming a septum nasi that lies wholly ventral to the trabeculae (Allis, 1917). In certain others of these fishes, this septum nasi is replaced by a median longitudinal ridge which extends forward from the basal-angle (Basalecke) across the subethmoidal depression. The basal-angle is said by Gegenbaur (1872, pp. 59 and 62) to be found, more or less developed, in the skulls of all of these fishes excepting only *Cestracion*, and it is shown lying ventral or ventro-posterior to the foramen opticum. On the dorsal surface of the trabecular plate there is, in all of these fishes, a cavum praecerebrale which communicates with the cavum cerebrale through a fenestra praecerebralis (Allis, 1913). The nasal apertures lie on the ventro-lateral edge of the snout, or on its ventral surface.

Comparing these conditions in the adult with those in early embryos, it is evident that the trabeculo-polar bars become greatly prolonged; that, in their growth forward, they pass lateral to the hypophysial pit, between its tip and external opening; and that they there leave the visceral-arch tissues in which they primarily lie and enter the frontal tissues, that is the space between the frontal ectoderm and the external surface of the brain, the latter surface being presented ventrally or antero-ventrally because of the still persisting cranio-cerebral flexure. Continuing their forward growth beyond this point, the trabeculo-polar bars fuse with each other, and as they pass ventral to the optic chiasma there bulge slightly outward, as shown in Sewertzoff's (1899) figure of *Acanthias* and in Goodrich's (1918) figure of *Scyllium*, this bulge forming the basal-angle. Continuing their growth forward beyond this point, the fused trabeculo-polar bars run antero-dorsally along the inclined surface of the brain, and pass between the nasal sacs at about the middle of their dorso-ventral extent, thus lying definitely dorsal to the nasal apertures. They then turn antero-ventrally beyond the sacs, and are more or less prolonged in a median rostral process.

Up to this stage of development the cranio-cerebral flexure has been but little reduced, and the frontal ectoderm is, from now on, anchored in place by the ingrowth of the trabeculo-polar bars. The cranial flexure cannot, therefore, be reduced, and the nasal capsules and nasal apertures retain their embryonic positions relative to the trabecular plate, the capsules lying lateral or latero-ventral to that plate and the apertures on the corresponding surface of the snout. The cerebral flexure can, on the contrary, be reduced, for the brain is not held in place by the trabeculo-polar bars as is the frontal ectoderm,

and when the anterior portion of the brain is withdrawn from its embryonic position on the dorsal surface of the trabecular plate, it leaves there the cavum praecerebrale, which thus prevents the formation of a septum nasi on the dorsal surface of the plate, between the nasal capsules.

The basal-angle (Basalecke) is said by Gegenbaur to lie always between those portions of the orbital walls that give articulation to the orbital processes of the palato-quadrates. These latter processes each lie on the dorsal edge of a dorso-anterior prolongation of the dorso-anterior corner of the epimandibular (palato-quadrate), and articulates with the premandibular part of the trabeculo-polar bar either directly or through the intermediation of a little cartilage described by Sewertzoff and Disler (1924) and considered by them to be the pharyngeal element of the mandibular arch. Comparison with the branchial arches of the Teleostomi would however seem to show, conclusively, that this little cartilage is either simply an articular one, or is the serial homologue of the infrapharyngo-branchials of the Teleostomi. Whether it be the latter element or not, what seems important is that either it, or the orbital process itself, articulates with the primitive pharyngeal element of the next anterior arch, as the infrapharyngo-branchials of the Holostei and Teleostei do, the trabecula and the polar cartilage thus each corresponding, in their respective arches, to the suprapharyngeal elements of the Teleostomi (Allis, 1925).

The mouth is actually or approximately ventral in all of the Selachii, and more or less so according as the orbital processes of the palato-quadrates articulate with the trabeculo-polar bars near the posterior or anterior end of the orbit. The cause of this ventral position is, primarily, the failure of the cranial flexure to be reduced before the trabeculo-polar bars have fused with the ventral surface of the parachordals, the palato-quadrates and mandibles consequently retaining to a considerable extent their embryonic positions, with the opening of the mouth directed ventrally.

All these several features of the Selachian skull are thus quite certainly related to a strong cranial flexure which is not reduced before the pharyngo-premandibulars have developed sufficiently to invade the frontal tissues and hold them in their embryonic positions.

In the Batodei, the conditions are probably similar to those in the Selachii, for the mouth is ventral, the nasal apertures lie on the ventral surface of the snout, and there is a rostral process and a cavum praecerebrale. I, however, know of no work that describes the fusion of the polar cartilages with the ventral surface of the parachordal plate, and there is no slightest indication, in the figures of the adult skull, of such a fusion, and no indication of either a basal-angle or a pituitary fossa.

In *Acipenser*, the polar cartilage of either side is said by Sewertzoff (1923) to fuse with the ventral surface of the parachordal, as it does in the Selachii, but this fusion must be due to some other cause than in the Selachii, for there is but little cranial flexure in early embryos of *Acipenser*. The external end of the hypophysial canal of embryos lies between the neuropore and the

adhesive organ (Haftscheibe) of von Kupffer's (1893) descriptions, and as the hypophysis of the adult lies in the cranial cavity, the hypophysial canal must have passed upward between the trabeculo-polar bars, as it does in the Selachii. The barbels of the adult are said to be developed from the adhesive organ, and they lie on the ventral surface of the snout, ventral to the ethmoidal expansion of the trabeculae. The nasal sacs lie on the dorsal surface of the latter cartilage, and the nasal apertures on the dorsal surface of the snout (Parker, 1882).

It is therefore certain that the trabeculo-polar bars of *Acipenser*, in growing forward, pass lateral to the hypophysial canal, slightly ventral to the definitive hypophysis, as they do in the Selachii, and there enter the frontal tissues. Anterior to this point the trabeculo-polar bars fuse with each other to form the related part of the basis cranii and the ethmoidal plate, the latter plate lying dorsal to that part of the adhesive organ from which the barbels develop, and hence quite certainly internal (dorsal) to the tissues resulting from the disintegration of the related portion of the hypophysial canal. The nasal sacs and nasal apertures lie, because of the slight cranial flexure, on the dorsal surface of the snout, and hence dorsal to the ethmoidal plate. Beyond this point, the ethmoidal plate, as it continues its forward growth, quite certainly pushes onward before it the tissues that represent the extreme anterior portions of the adhesive organ and the hypophysial cord, these tissues retaining their embryonic positions on the top of the snout and hence lying anterior to, and on the dorsal surface of, the tip of the ethmoidal plate. Further evidence in favour of this is the course of the related portions of the infraorbital latero-sensory canals of this fish as compared with that of the same canals in the Selachii.

In the Selachii, *Mustelus* being taken as a type, the infranasal portion of the infraorbital canal lies on the ventral surface of the snout, and there meets and fuses, in the median line and between the nasal apertures, with its fellow of the opposite side (Allis, 1901). The median canal so formed extends forward a short distance, and then separates into two parts, one on either side, each of which runs forward and fuses, at the edge of the snout, with the corresponding supraorbital canal. The point where the hypophysial pit primarily opened to the exterior, lies in the buccal cavity and hence posterior to the point where the infranasal canals fuse with each other in the median line, these canals thus lying wholly in what I have characterised as frontal tissues. The visceral-arch tissues do not extend forward even to the anterior edge of the mouth. In *Acipenser*, the corresponding parts of the infraorbital canals do not meet and fuse on the ventral surface of the snout, each canal first running forward along the lateral edge of the space between the mouth and the barbels, then turning mesially anterior to the barbels, and then forward to the anterior end of the ventral surface of the snout, lying, in the latter part of its course, parallel to, and but slightly distant from, its fellow of the opposite side (Allis, 1904). At the anterior end of the snout the canal turns

upward and then mesially, and crossing the dorsal surface of the tip of the snout runs directly into, and is continuous with, its fellow of the opposite side. As the canal turns mesially on the tip of the snout, a short canal is sent dorso-postero-laterally and apparently corresponds to that terminal portion of the canal of *Mustelus* that anastomoses with the supraorbital canal.

Comparing these canals in these two fishes, the suggestion is evident that the canals of *Acipenser*, like those of *Mustelus*, remain in the frontal tissues to which they are primarily related, avoiding the visceral-arch tissues concerned in the formation of the adhesive organ and the ventral wall of the hypophysial pit, and that these latter tissues are continued forward in the median line to the tip of the snout. The tissues that represent the primitive point of attachment of the hypophysial pit (or canal) therefore lie, in the adult, on the dorsal surface of the snout, immediately anterior to the ethmoidal cross-commissure of the infraorbital canals. The trabeculae of this fish thus certainly lie everywhere dorsal (internal) to the anterior portion of the hypophysial canal.

The basal-angle of the Selachii is considered by Sewertzoff (1923) to be represented, in *Acipenser*, in the ventro-posteriorly directed hind end of a median longitudinal ridge on the ventral surface of the ethmoidal portion of the neurocranium. This ridge is well shown in Parker's (1882) figures of *Acipenser*, and there, as well as in Sewertzoff's figure, it lies wholly anterior to the pituitary fossa, to the optic foramina, and to processes on the orbital wall that are said by Sewertzoff to give attachment to ligaments that hold the palato-quadrate up against the ventral surface of the skull, and that are therefore considered by him to be the homologues of the surfaces that give articulation to the orbital processes of the palato-quadrates of the Selachii. The so-called basal-angle of *Acipenser* therefore does not have, to these several structures, the characteristic topographical relations of the basal-angle of the skull of the Selachii, and it would seem to correspond to the process V of Gegenbaur's descriptions of the latter fishes, which he calls the "mediane Leiste des Internaselknorpels."

The mouth of *Acipenser* is ventral, as it is in the Selachii, and this would seem to be related to the fusion of the polar cartilage with the ventral surface of the parachordal. The mouth of *Acipenser* could not, however, have been directly derived from that of the Selachii, for the suspension of the jaws is teleostean in character (Allis, 1925), and the external opening of the hypophysial pit lies external to the buccal cavity.

In the Holostei, the pharyngeal elements of the mandibular and premandibular arches swing upward into the plane of the parachordals before fusing with the latter cartilages or with each other, and the pharyngomandibulars then fuse with the anterior ends of the parachordals, instead of with their ventral surfaces. This is evidently due, in part, either to the slight cranial flexure or to its relatively early reduction, but this does not explain why this end to end fusion takes place in these fishes and not in *Acipenser*, where there is also but little flexure.

In both *Amia* and *Lepidosteus* there is an adhesive organ on the anterior end of the snout, and it is considered to be strictly homologous with that of *Acipenser*. In embryos of *Amia*, the point of attachment of the hypophysis to the ectoderm lies between this adhesive organ and the neuropore, as it does in *Acipenser*, but Reighard and Mast (1908) say that the fundament of the organ of *Amia* is solid and not an invagination. The hypophysis of the adult lies in the cranial cavity, and the nasal capsules and nasal apertures lie on the dorsal surface of the snout. In *Lepidosteus* the conditions are doubtless similar. The trabeculo-polar bars of these two fishes must therefore pass forward lateral to the hypophysial cord, as they do in *Acipenser*, and then enter the frontal tissues. There they certainly, at first, lie dorsal to the hypophysial cord, but there is nothing in the descriptions to show definitely that they retain that relation to it. It is, however, quite certain that they do. In two figures of sagittal (longitudinal vertical) sections of 18 mm. and 20 mm. larvae of *Amia*, Reighard and Phelps (1908) show a cartilage which they call the "superior maxillaries" and also the "cartilage of the upper jaw." This cartilage is the ethmoidal (orbito-nasal, Pehrson) plate, and it is shown lying ventral to the ethmoidal cross-commissure of the infraorbital latero-sensory canals. This commissure lies slightly posterior to the adhesive organ, and the hypophysial cord must have passed inward between these two structures, for it lies, in earlier embryos, close against the posterior surface of the adhesive organ. The latter organ has the appearance of turning upward over the anterior end of the ethmoidal plate, and if that be so, the hypophysial cord must have had a similar course. The ethmoidal cross-commissure has a curved course over the tip of the snout, as in *Acipenser*, and the relations of this canal and the ethmoidal cartilage to the hypophysial cord (or canal) is quite certainly the same in these two fishes.

In the Crossopterygii and Teleostei the trabeculo-polar bars probably always fuse with the anterior ends of the parachordals, as they do in the Holostei, but this has been definitely determined in only a few forms. The nasal sacs lie on the dorsal surface of the ethmoidal (orbito-nasal) plate, and the nasal apertures on the dorsal surface of the snout. In *Polypterus* the external opening of the hypophysial pit lies in the roof of the buccal cavity (Kerr, 1907), and it is probable that it has a similar position in the Teleostei, for Kerr says (1919, p. 142), in a statement referring to all the non-mammalian vertebrates, that the hypophysis "arises normally as an ingrowing pocket of ectoderm close to the hinder limit of the stomodaeum but in the case of the Cyclostomes just outside its anterior boundary." Goodrich however says (1917, p. 545): "That the hypophysis is an ancient organ which must have been possessed by the ancestor of all the Craniates is shown by its constant presence and uniform development. Invariably it arises as an ingrowth of ectoderm just in front of the mouth and just anterior to the front end of the archenteron." These two statements are not wholly in accord, but however this may be, it is certain that the trabeculo-polar bars of these fishes, in

growing forward, pass lateral to the stalk of the hypophysis and, entering the frontal tissues, lie always either wholly anterior to the pit, or dorsal to its anterior portion. Because of the slight cranial flexure, the ethmoidal (orbito-nasal) plate passes ventral to the nasal sacs and nasal apertures.

In *Polypterus* there are adhesive (cement) organs, as there are in the Ganoidei, but as these organs are of visceral-arch origin, and the visceral-arch tissues only extend forward to the ventral (posterior) edge of the hypophysial pit, the organs lie on either side of the head, lateral to the mouth opening, instead of on the anterior end of the snout; and apparently correlated to this, the ethmoidal cross-commissure of this fish runs straight across the anterior end of the snout, instead of curving upward and backward (Allis, 1922). In the Teleostei, no adhesive organs have as yet been described (Kerr, 1919, p. 182), and so far as I know there is no ethmoidal cross-commissure in any of these fishes.

In the Cyclostomata the trabeculo-polar bars fuse with the anterior ends of the parachordals, as they do in the bony fishes, and the single nasal capsule and single nasal aperture lie dorsal to the trabeculae, as also in the bony fishes. The external opening of the hypophysial canal lies on the dorsal surface of the snout, as in the Ganoidei, and the hypertrophied upper lip of the cyclostomes has been compared with the adhesive organ of the ganoids. The hypophysial canal of the Cyclostomata, however, runs posteriorly dorsal to the trabeculae and the plates that develop in relation to them, instead of ventral to those structures, and then passes downward between the trabeculo-polar bars, where, in the Petromyzontidae, it enlarges into a sac beneath the brain, and in the Myxinoidei opens backward directly into the pharynx (Goodrich, 1909). The hypophysis of the adult lies, as in other fishes, in close relation to the infundibulum.

Comparing these conditions in the Cyclostomata with those in the Ganoidei, it seems certain that the trabeculo-polar bars, in growing forward, first pass lateral to the hypophysial canal slightly ventral to the adult hypophysis, as in all other fishes, but then, instead of continuing onward in the frontal tissues, they re-cross the canal and re-enter the visceral-arch tissues of the upper lip. There the trabeculae (pharyngo-premandibulars) articulate with the epipremandibulars, and the latter elements articulate with the ceratopre-mandibulars (Allis, 1924 *a*), these several elements having their primitive dorso-ventral relations to each other and not the sigma-form relation. The polar cartilage and palato-quadrate have, on the contrary, the sigma-form relation to each other, at least in the Myxinoidei; and that these cartilages of the mandibular arch could have independently acquired this form, which is related to a biting jaw, while the cartilages of the premandibular arch retained their primitive dorso-ventral relations, seems wholly impossible. The cyclo-stomean condition could, however, have been readily derived from the ganoidean one, by the simple shifting downward of the trabeculo-polar bars before the trabecular (ethmoidal) plate had been developed. The cartilages

of the premandibular arch would then have re-acquired their primitive dorso-ventral relations to each other in connection with the development of the lips.

A deep hypophysial pit is not a primitive feature, for as it has arisen, if my theory is correct, by the rolling together of frontal and visceral-arch surfaces, the shorter the pit the more primitive the condition. In both the Cyclostomata and the Ganoidei this rolling together of the two surfaces has continued until the neuropore is reached, and in the Cyclostomata the olfactory placodes have become enclosed in the large external opening of the pit, there lying in the frontal tissues and hence in the dorsal wall of the pit. Because of their enclosure in the pit, the placodes are held close together, and the single median olfactory organ arises.

It is thus seen that, in so far as the features here under consideration are concerned, the Cyclostomata are much more closely related to the Ganoidei than to either the Plagiostomi or the Teleostei, and it is to be further noted that, in the Petromyzontidae, the muscles of the eyeball are innervated on the ganoidean pattern, which differs from that in both the Plagiostomi and the Teleostei. It is therefore probable that the Cyclostomata are highly specialised, and not primitive forms.

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ON THE HYOMANDIBULA OF SELACHII, TELEOSTOMI AND *CERATODUS*

By F. H. EDGEWORTH, M.D.

The theory of Gegenbaur that the hyomandibula in Teleostomi is homologous with that in Selachii has not found universal acceptance in recent years, and other theories have been advanced, by Allis, Schmalhausen, and de Beer.

As I am still an adherent to the old theory, I think it may be well to advance some criticisms of these newer doctrines and to give reasons for not adopting them. The conditions in *Ceratodus* have been brought within the scope of these theories, and I have accordingly analysed the statements made.

CERATODUS

As a preliminary to the following discussion it may be remarked that in October 1923 I stated and gave evidence that in a 13·0 mm. embryo of *Ceratodus* there is a procartilaginous tract—the epihyale—extending from the dorsal end of the keratohyale upwards and inwards beneath, though not at first attached to, the ventral surface of the auditory capsule. This epihyale separates into three portions—from above downwards, the oto-quadrate cartilage, the interhyale, and the hyosuspensorial ligament. The first-named gains attachments—its inner end to the base of the chondrocranium and its outer end, subsequently, to the quadrate. The interhyale becomes a saddle-shaped cartilage on the anterior edge of the Levator hyoidei. The ligament slowly extends forwards to the quadrate.

I may add that I had serial sections of embryos of 11, 12, 13, 13·5, 14, 14·5, 15, 16, 16·5, 17·5, 19, 20, 24, 27 and 28 mm. in length, so that the developmental changes could be followed with a fair amount of certainty. I was thus enabled to "place" the various structures described by previous investigators, each of whom, apparently, had but one or two late stages for examination.

I regret that I did not refer to the paper of Allis which, published in 1915, escaped my notice. Schmalhausen's paper was published in July 1923, whilst my paper was in the press; de Beer's was published in 1924.

Allis, who did not, however, make any embryological investigations, was of opinion that there is in *Ceratodus* a hyomandibula which is formed by fusion of an interarcual cartilage with a pharyngohyale. This hyomandibula is the cartilage which I called "oto-quadrate." It has the development I described, and is not formed by fusion of two cartilages. He also stated that the hyomandibula of Huxley is probably the extrabranchial of the hyal arch. This is not possible, as the cartilage—which I called "interhyale"—is one of the three portions into which the epihyale separates.

Schmalhausen's interpretation of the conditions found in his embryo does not seem to be quite accurate. The sections had been lent to him by Professor Sewertzoff. Now this embryo, as I showed from quite other structures, was almost certainly not one of Semon's stage 47 (– 15·7 mm.), but slightly older than stage 48 (– 17·8 mm.). This conclusion is in harmony with Schmalhausen's description of the primordium of the operculum—which I find first visible in a 17·5 mm. embryo as a thin plate of cells external to the Levator hyoidei.

Schmalhausen described three cartilages above the keratohyale—the hyomandibula, pharyngohyale and interhyale. He also depicted the Levator hyoidei passing from the floor of the auditory capsule to the interhyale. This cartilage is that to which I also, independently, gave the same name. I do not find, however, that the Levator hyoidei is inserted into it. In the embryos I have examined it is inserted into the keratohyale (*vide* figs. 21 and 22). Schmalhausen's "hyomandibula" is, I think, probably the slightly downturned lateral edge of the auditory capsule. In none of the embryos which I have examined is this lateral edge of the auditory capsule separated off. It is not, as he suggests, the "hyomandibula" of Huxley and Sewertzoff, for this cartilage is, as they stated, partially embedded in the hyosuspensorial ligament—and this is true of the interhyale both in the embryo and the adult.

Schmalhausen's "pharyngohyale" is the cartilage which I called "oto-quadrate." It is, as he says, attached to the floor of the auditory capsule. He did not describe any connection of its outer end with the quadrate. This is correct, for this does not occur, in the embryos I have, until the 20 mm. stage. He further states that the pharyngohyale is the cartilage called "hyomandibula" by K. Furbringer, Krawetz and Greil. I think this only probable, not quite certain, as regards Greil, who did not describe any connection with the auditory capsule of the inner of his two epihyalia (hyomandibularia).

Schmalhausen further states that "von aussen liegt am dorsalen Ende des Hyoids ziemlich nähe die Anlage des Operculum." My observations agree with this, and I would merely add that this primordium is the Zellenstrang of Greil—to be referred to later.

de Beer stated that in a 13 mm. embryo of *Ceratodus* "there is a very small hyomandibular articulating halfway between the notochord and the edge of the auditory capsule, median to the vein and the muscle." "Lateral to the muscle is the strand of rudimentary procartilage described by Greil." I would first remark that the "hyomandibular" of the above description is my "oto-quadrate"; the vein is the vein which I, following Kellicott who first described it in the embryo, called "anterior cardinal"; and the muscle is the "Levator hyoidei" of Greil, whose nomenclature I followed.

Now, I do not think the above statements can be accepted, for (1) I have not, in the many embryos examined, found the oto-quadrate cartilage "articulating" with any other structure. Its inner end becomes continuous with the floor of the auditory capsule, and its outer end subsequently with the quadrate—as I stated and depicted; (2) the oto-quadrate cartilage is one of the products of

separation of the epihyale into parts, and therefore the interhyale should have been present if the embryo were normal. There is, however, no mention of it, nor is it figured; (3) the "Zellenstrang" of Greil does not deserve the name of procartilage, for it does not develop into cartilage, but is the primordium of the (osseous) operculum. Greil's earliest and only embryo in which he described this strand was one of 17·8 mm. He did not investigate any later stages, and his statement that it "stellt wohl die Anfänge kleiner Vorknorpelherde dar" is a mere surmise.

de Beer states that the cartilage which I called "interhyale" is "obviously the structure produced by the Zellenstrang of Greil." This is not correct, for I stated that the interhyale is chondrified in a 16·5 mm. embryo, i.e. at a stage when the Zellenstrang is not yet visible, and indeed chondrification begins at a still younger stage—in an embryo of 15 mm. Further, I stated that the interhyale is the outer of the two cartilages described by Greil in his 17·8 mm. embryo (i.e. the embryo which additionally had the Zellenstrang), and called by him "epihyalia." This statement should, I think, have been mentioned, possibly even discussed, before proposing a theory which is untenable.

I am, then, of opinion that de Beer mistook the procartilaginous or cartilaginous (according to the stage he had) interhyale, which sits saddle-wise on the anterior edge of the Levator hyoidei, for the non-cartilaginous primordium of the operculum which is developed, at a later stage, on the external side of that muscle. My series of embryos thus suggests that de Beer's 13 mm. specimen was either abnormal, or in part abnormal and in part misinterpreted.

de Beer also states that I did not give the relations of the interhyale to the vena capitis. This remark, however, is hardly justifiable, for in figs. 35, 36 and 37 of my paper I depicted the vein lying dorsal to the inner part of the oto-quadrate cartilage, i.e. in exactly the same position as he subsequently showed it.

To show the relations of the Levator hyoidei to the interhyale, the tr. hyomandibularis vii, and the operculum, I give figures drawn from models made of these structures.

In the 15 mm. embryo (fig. 21) there is no operculum. The Levator hyoidei arises from the ventral surface of the auditory capsule and passes down to the upper end of the keratohyale. The hindmost fibres pass down a little way along its posterior edge. In front of the Levator hyoidei are the interhyale and the hyosuspensorial ligament. The former is a narrow disk-like cartilage. The ligament passes forward from the upper end of the keratohyale, but does not yet reach the quadrate. The tr. hyomandibularis vii passes down in front of the interhyale and external to the ligament.

In the 20 mm. embryo (fig. 22) the interhyale has become < shaped. Its outer limb—which is longer than the inner one—is external to the anterior part of the Levator hyoidei, and its inner limb is internal. The primordium of the operculum is external to the Levator hyoidei. The hyosuspensorial ligament reaches the quadrate.

(It might be supposed, on comparison of figs. 21 and 22, that the shapes of the quadrate and keratohyale are somewhat different in the two specimens. They are really very similar. The difference in the drawings is due to the fact that fig. 21 is a lateral view, whereas fig. 22 is an antero-lateral one. The latter had to be as it is, to show the fibres of the Levator hyoidei between the operculum and the interhyale. In a purely lateral view these fibres are not visible, owing to the anterior edge of the operculum almost overlapping the posterior edge of the outer limb of the interhyale. The oto-quadrate cartilage is, of course, not visible in these lateral views of the models.

THE THEORY OF SCHMALHAUSEN

Schmalhausen stated that in *Acipenser* embryos there is, at the base of the cranium, a bridge which forms the ventral wall of a short canal in which are situated the tr. hyomandibularis vii, the vena jugularis, and the art. carotis externa (facialis?). The outer end of this bridge abuts on the hyomandibula.

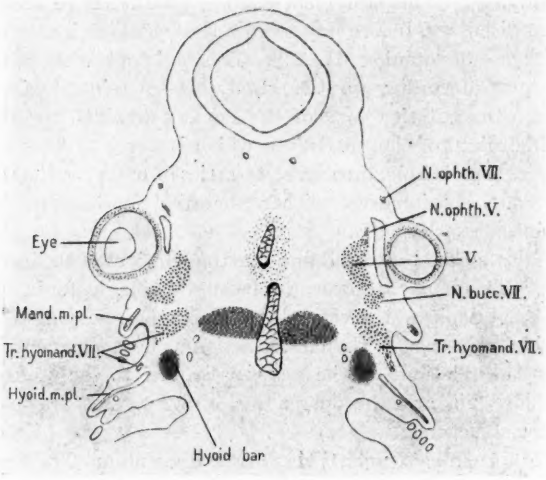

Fig. 1. *Scyllium canicula.* 27 mm., horizontal section.

This bridge is serially homologous with the pharyngobranchiale of the first branchial bar, and is a pharyngohyale. He takes this as his "Ausgangsform." In Selachii the hyomandibula represents the pharyngohyale and the ventral portion of the epihyale, the dorsal portion of the latter having disappeared. In Teleostomi the pharyngohyale has disappeared, and the hyomandibula represents the epihyale only.

No figure representing this pharyngohyale of *Acipenser* was given.

My difficulty in accepting Schmalhausen's theory is that, though a canal in the floor of the auditory capsule is present in a 19 mm. embryo, examination of earlier stages shows that it is developed otherwise than he supposed. In

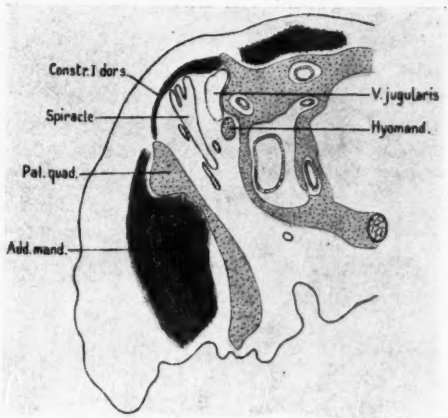

Fig. 2

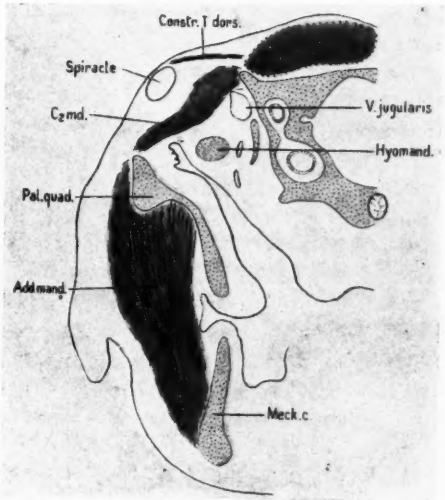

Fig. 3

Figs. 2 and 3. *Heptanchus cinereus.* 70 mm., transverse sections. Fig. 2 is the more anterior. There is a distance of ·68 mm. between the two sections.

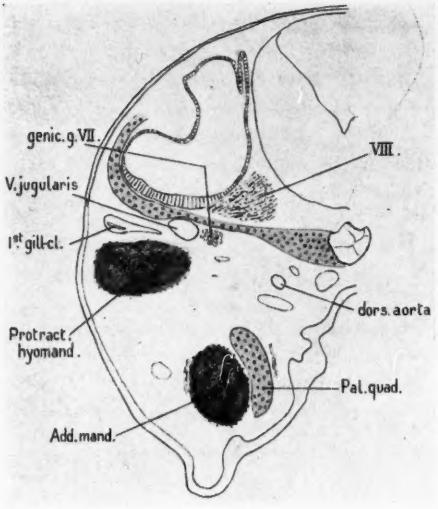

Fig. 4

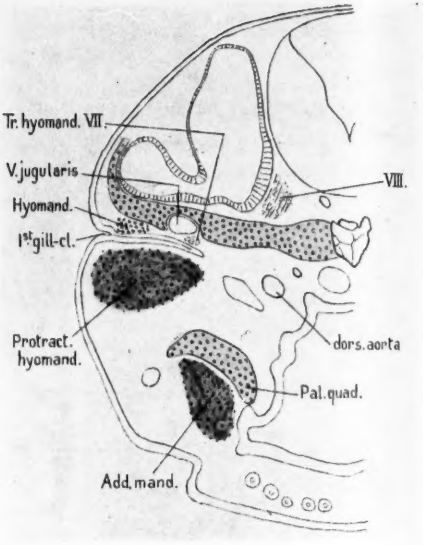

Fig. 5

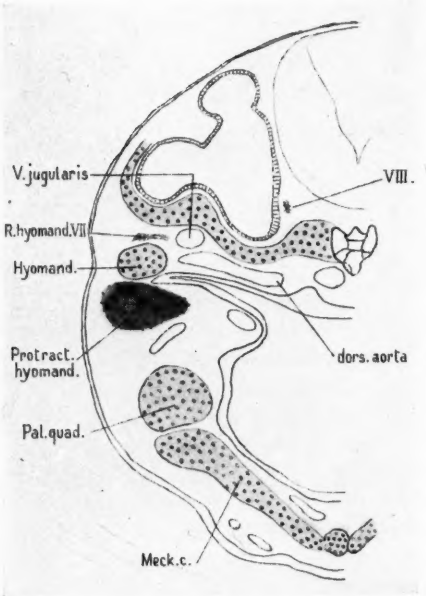

Fig. 6

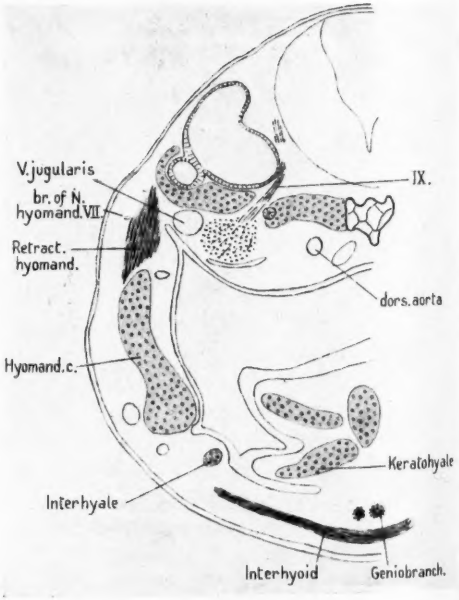

Fig. 7

Figs. 4–7. *Acipenser ruthenus.* 11 mm., transverse sections. Fig. 4 is the most anterior. There is a distance of ·032 mm. between figs. 4 and 5, ·072 mm. between figs. 5 and 6, ·064 between figs. 6 and 7.

an 11 mm. embryo (figs. 4–7) the chondrified floor of the auditory capsule is, anteriorly, flat. A little further back (fig. 5) the head of the hyomandibula abuts against the outer part of the floor. Internal to this there is a groove in the floor. A little further back (fig. 6) the groove becomes more and more shallow, and the floor is simply concavo-convex from without inwards. Further back (fig. 7) the floor is slightly convex. The tr. hyomandibularis vii passes from the geniculate ganglion backwards, then outwards, and then outwards and slightly forwards above the head of the hyomandibula. The vena jugularis passes backwards in the groove, dorsal to the tr. hyomandibularis vii.

In a 15 mm. embryo (fig. 8) the groove is closing in, by growth from its ventro-internal and ventro-external edges. In a 19 mm. embryo (figs. 9–12) a canal is formed, ·25 mm. long and ·08 mm. broad. Its floor is formed by a

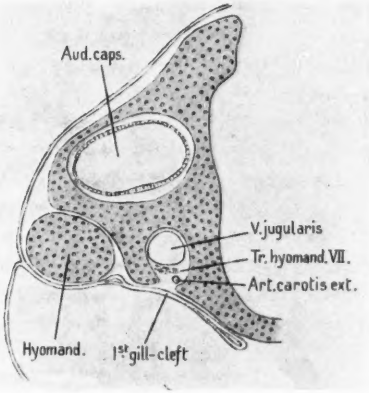

Fig. 8. *Acipenser ruthenus.* 15 mm., transverse section.

slightly oblique cartilaginous bridge passing inwards and slightly backwards. The canal transmits the tr. hyomandibularis vii, the art. carotis externa, and the vena jugularis. This art. carotis externa of Schmalhausen is a branch of the dorsal aorta at the level of the upper end of the first branchial bar. It passes outwards and forwards into the canal, and then, at its anterior end, forwards and downwards between the Protractor hyomandibulae and the Adductor mandibulae.

The canal is thus developed by the formation and closing in of a groove on the ventral surface of the auditory capsule, and is not due to the fusion of any pharyngohyale with the floor[1]. I cannot find any trace of any structure which might be interpreted as a pharyngohyale.

I may add that, though there is no description of this groove or canal on the floor of the auditory capsule of *Acipenser* embryos in the account given by

[1] All these structures are excellently shown in the models of the chondrocranium of these embryos which my colleague Dr Henderson has recently been making.

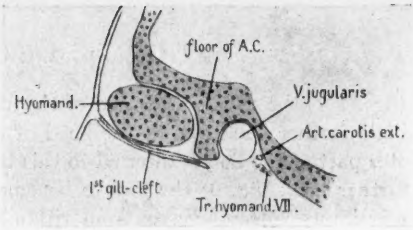

Fig. 9

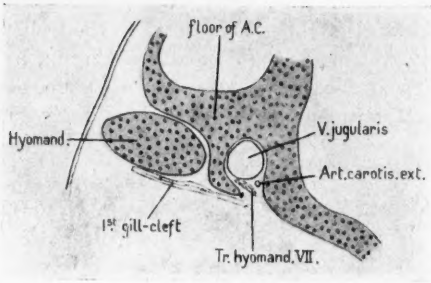

Fig. 10

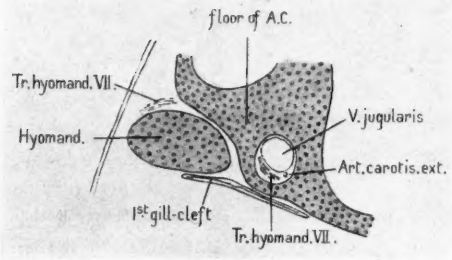

Fig. 11

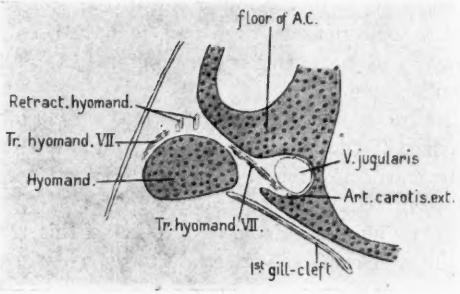

Fig. 12

Figs. 9–12. *Acipenser ruthenus.* 19 mm., transverse sections. Fig. 9 is the most anterior. There is a distance of ·06 mm. between figs. 9 and 10, ·04 between figs. 10 and 11, ·04 mm. between figs. 11 and 12.

W. K. Parker in 1882, yet the groove is depicted in his fig. 6 of Plate XV, and the canal in his fig. 8 of Plate XVII. The canal is also present in *Polyodon* and *Polypterus* (*vide* Allis, and fig. 13).

THE THEORY OF ALLIS

The theory of Allis (1915) in regard to the hyomandibula of Selachii and Teleostomi is as follows: The hyomandibula of Selachii is formed by an epihyal. That of *Amia*, *Lepidosteus*, and Teleostei, is formed by the fusion of anterior and posterior portions. The anterior portion is derived from an interarcual cartilage between the hyal and mandibular arches. This opinion was subsequently (1918) modified, and the anterior portion was said to represent the anterior branchial-ray bar of the hyal arch. The posterior portion is derived from the dorsal extra-branchial of the hyal arch.

Now I had stated (1911) that "in *Lepidosteus*, *Amia*, and *Salmo*, the viith nerve, at first winding round the hyoid bar, subsequently pierces the hyomandibula owing to chondrification spreading round it; the more primitive condition is preserved in *Acipenser* and *Polypterus*."

Allis was of opinion that this chondrification spreading round the tr. hyomandibularis vii "is simply the chondrification in situ of the extrabranchial of the arch and its concomitant fusion with the pharyngohyal."

In the Chondrostei the hyomandibula articulates with the auditory capsule by one head. This was regarded as indicating that the posterior constituent is more or less completely aborted. His opinion of the conditions in *Polypterus* is cited below.

In a 7·75 mm. embryo of *Amia* (fig. 14) the hyoid bar is a continuous structure in a procartilaginous condition, and lies just behind the 1st gill-cleft. The hyomandibular part of it is, as seen in horizontal section, oblong in shape. The tr. hyomandibularis vii passes outwards behind it. There is no trace of any additional skeletal element behind the nerve.

In a 8·0 mm. embryo (figs. 15–17) the upper part of the hyomandibular part of the hyoid bar has extended backwards, and, in horizontal section, forms an antero-posterior plate. The nerve pierces it. Neither above (fig. 15) nor below (fig. 17) is any evidence present that any additional element has fused with the posterior edge of the first formed portion.

In *Polypterus* the tr. hyomandibularis vii separates into its r. mandibularis and r. hyoideus anterior to the hyosymplecticum; its r. mandibularis passes in front of the hyosymplecticum and its r. hyoideus behind. Allis stated that in a 75 mm. specimen "there is a small and independent bit of cartilage lying immediately posterior to the cartilage that caps the actual articular head of the hyomandibula and the so-called accessory hyomandibula is developed in relation to it." In the adult "a stout ligament extends from the accessory hyomandibular to the dorsal edge of the opercular process of the hyomandibular and lies posterior to the nervus hyoideus facialis; this ligament and the accessory hyomandibular quite certainly representing the posterior articular

head of the teleostean hyomandibular." It was not stated whether this ligament is present in his 75 mm. specimen.

Budgett showed, in a 30 mm. specimen of *Polypterus*, the hyomandibula abutting against the lateral surface of the auditory capsule with a large

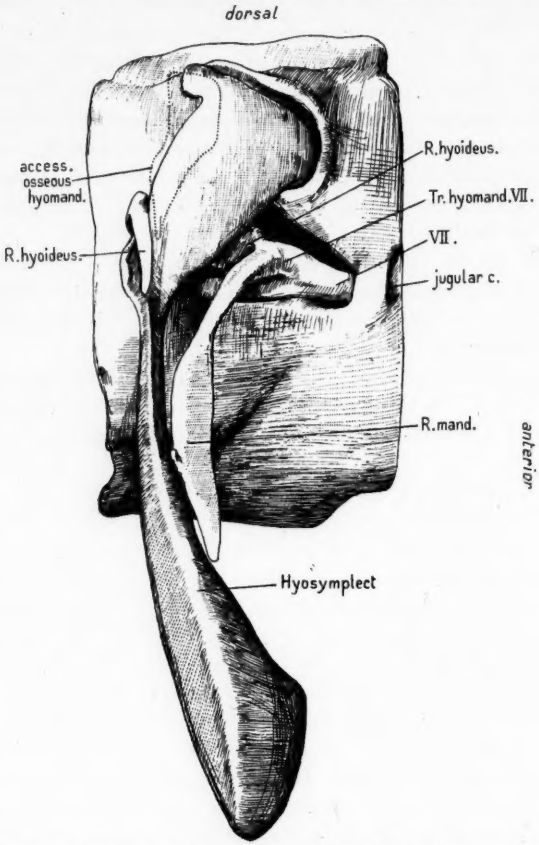

Fig. 13. *Polypterus senegalus*. 75 mm., lateral aspect of model of hyosymplecticum and part of the auditory capsule. The osseous accessory hyomandibula is indicated only by dotted lines. In the model it is removable.

rounded head. A rod of cartilage is attached to the posterior surface of the hyomandibula. This persists in the inner surface of the opercular bone.

I find in a 75 mm. specimen (fig. 13) a specimen[1] which, though of the same length as that of Allis, was apparently younger—that the hyosymplecticum is a slightly curved rod, concave anteriorly. This cartilage I call "hyosymplecticum" as it is homologous with the primordium of the hyomandibula

[1] I described the cranial musculature of this specimen in 1911.

and symplecticum of *Acipenser*, *Amia*, and *Lepidosteus*[1]. Its broad head articulates with a depression in the lateral surface of the auditory capsule. The depression has a dorsal pterotic edge. From the upper part of the head a short process projects backwards. It takes part in the articulation. It is continuous with the main part of the articular head. The (osseous) "accessory hyomandibula" fits on the back of the head of the hyosymplecticum and the lateral surface of its posterior process. It is a covering bone and separated from the cartilage by a slight cleft, and appears different in nature from the (osseous) hyomandibula which is inseparable from the underlying cartilage. The viith nerve issues from the ventro-lateral surface of the auditory capsule into the jugular canal, and passes backwards. It gives off the r. hyomandibularis which immediately separates into the r. mandibularis passing in front of

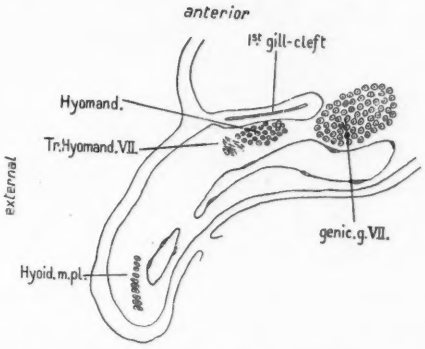

Fig 14. *Amia calva*. 7·75 mm., horizontal section.

the hyosymplecticum, and the r. hyoideus passing behind it. The jugular canal also contains the vena jugularis. There is no ligament such as Allis described in the adult passing from the accessory hyomandibula to the opercular process of the hyomandibula.

On comparison of these three specimens in the order of their development—those of Budgett, of myself and of Allis—it appears that the small and independent bit of cartilage described by Allis is due to separation of a posterior process of the head of the hyomandibular from the remainder, and is not an originally separate cartilage. It is formed quite late in development, and subsequently separates. The (osseous) "accessory hyomandibula" is not exclusively related to the cartilaginous process. It is of much wider extent, and is for the most part a covering bone for the dorsal posterior part of the hyosymplecticum. The ligament described by Allis is formed still later and has no relations to the bit of cartilage. The theory that the separated bit

[1] I shall be describing the interesting earlier stages in the development of this cartilage in a future publication.

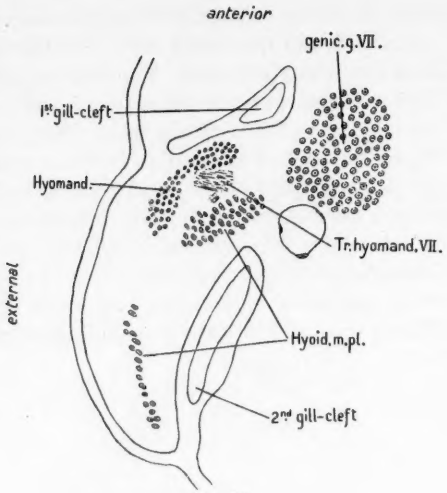

Fig. 15

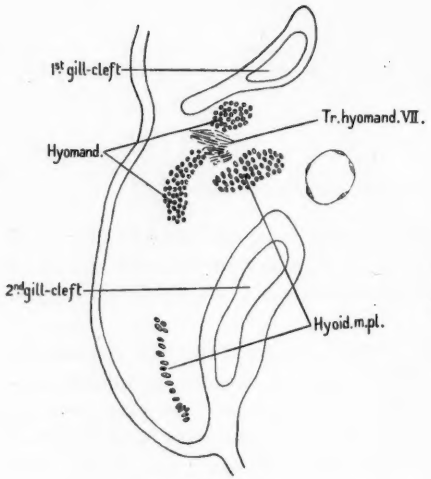

Fig. 16

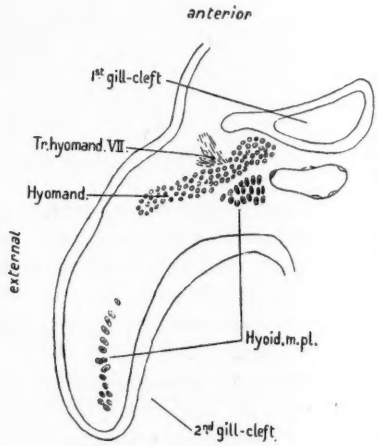

Fig. 17

Figs. 15–17. *Amia calva.* 8 mm., three successive horizontal sections, each ·008 mm. thick. Fig. 15 is just above the foramen for the tr. hyomandibularis vii, fig. 16 through it, fig. 17 just below it.

of cartilage and the ligament represent a separate morphological unit appears incompatible with these facts[1].

In a 5 mm. embryo[2] of *Salmo trutta* (fig. 19) the primordium of the hyomandibular part of the hyoid bar lies immediately behind the 1st gill-cleft. The tr. hyomandibularis vii passes outwards behind the hyomandibula, which does not extend behind the nerve.

In a 5·5 mm. embryo (fig. 20) the upper part of the hyomandibular portion of the hyoid bar has extended backwards, forming a plate, and the tr. hyomandibularis vii perforates it. The 1st gill-cleft is beginning to form.

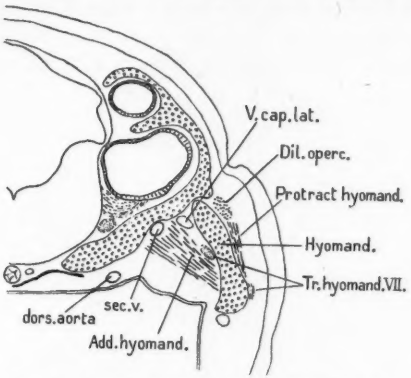

Fig. 18. *Lepidosteus osseus.* 19 mm., transverse section.

In a 6·5 mm. embryo chondrification has taken place. The plate-like upper portion of the hyomandibular portion of the hyoid bar does not show any trace of being formed by the coalescence of two skeletal portions.

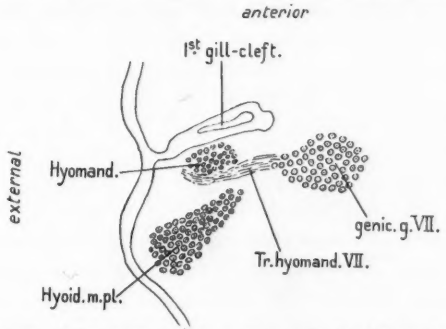

Fig. 19. *Salmo trutta.* Embryo, 5 mm., horizontal section.

In many Teleostei the hyomandibula articulates by two heads with the

[1] Allis's statement that "in *Polypterus* the hyomandibular is said by Edgeworth to develop exactly as in *Acipenser*" is incorrect. I made no such statement. In fact I said (p. 207) "The development is not yet known in *Polypterus*."

[2] I cannot be sure of the exact lengths of these embryos, owing to their curving round the yolk.

auditory capsule. Allis considered these two heads to represent the two skeletal elements of which he considered the hyomandibula to be formed.

de Beer, who adopted Allis's theory (*vide infra*), cited Swinnerton's investigations on *Gasterosteus* in support of it.

Now Swinnerton stated that, in his stage i, the hyomandibula and symplectic together form a continuous chondrified plate. The tr. hyomandibularis vii perforates the former element. In stage iii the articulation of the hyomandibula with the auditory capsule "begins to depart from the simple elongated type of earlier stages, and which is retained by many Teleosts, e.g. salmon; and to take on that two-headed type of articulation seen in the pike and so commonly possessed by Acanthopterous fishes." In stage iv "the articulating border has differentiated still more distinctly into two articular heads."

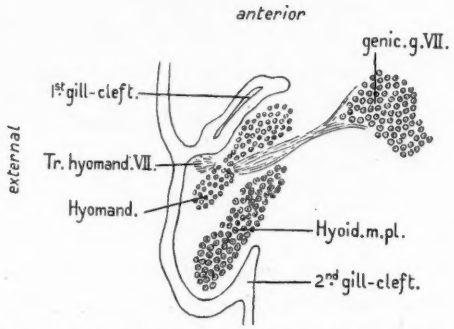

Fig. 20. *Salmo trutta.* Embryo, 5·5 mm., horizontal section.

Swinnerton thus described only one cartilage with one articular head, which gradually develops into two articular heads. If the posterior articular head of the hyomandibula and the portion of the cartilage posterior to the foramen for the tr. hyomandibularis vii represent an added skeletal element, it might be expected that some evidence of fusion of two skeletal elements would be present in the portion of hyomandibula between the foramen and the articular head or heads, especially during those stages of development in which two heads are being formed.

Professor Swinnerton was good enough to give me embryos of Gasterosteus aculeatus of his stage i, ii and iii. Horizontal sections show no trace of fusion of two skeletal elements—the cartilage is absolutely uniform in appearance right through from front to back.

Similar results were found in embryos of *Caranx trachurus.* It would thus appear that whereas in *Acipenser* and *Polypterus* the hyomandibula or hyosymplecticum—as seen in horizontal section—is a transverse oval, i.e. is a rod, at the point where the tr. hyomandibula vii or its r. hyoideus passes behind it; on the other hand in *Amia* it is at first similarly a rod, the nerve

passing behind it, and subsequently extends backwards so that, in horizontal section, it becomes a plate, the nerve passing through a foramen in it. No evidence was seen, either in the embryos depicted or in others of the same stages, that the development of a plate is due to the fusion of any additional cartilage. Its formation is simply due to backward growth or extension of the first-formed portion of the bar.

Allis's theory thus fails unless he can give evidence, in some developing Teleostome, of the existence of an originally separate procartilaginous or cartilaginous structure posterior to the r. hyomandibularis vii which

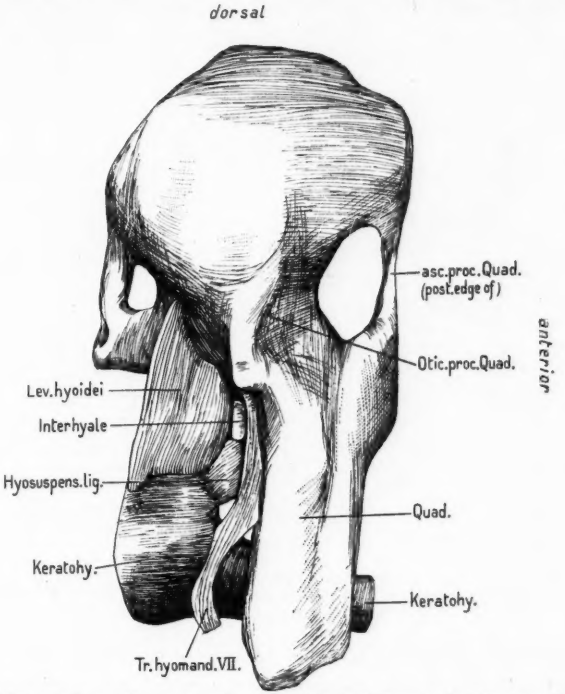

Fig. 21. *Ceratodus.* Embryo, 15 mm., drawing of model of the Levator hyoidei, etc., lateral aspect.

subsequently fuses with the hyomandibula. It is for him, having suggested the theory, to offer such evidence. Unless this be done my observation, published in 1911 and confirmed in this paper, that in the fish examined the foramen is due to an extension backwards of the cartilage involving the nerve affords a simple and adequate explanation of its occurrence.

The development of two articular heads to the hyomandibula in *Gasterosteus* and *Caranx* is brought about by a gradual development of the long area of contact of the hyomandibula with the auditory capsule into two articular heads, and is not due to the fusion of any additional cartilage.

THE THEORY OF DE BEER

de Beer expressed the opinion that the hyomandibula of Selachii is a "true hyomandibular," but did not indicate what was to be understood by the adjective "true." He adopted Allis's 1915 theory in regard to the hyomandibula of Teleostomi. The only change made in the nomenclature was that the supposed posterior constituent of the hyomandibula was termed "processus oticus hyomandibularis." I have discussed this theory above.

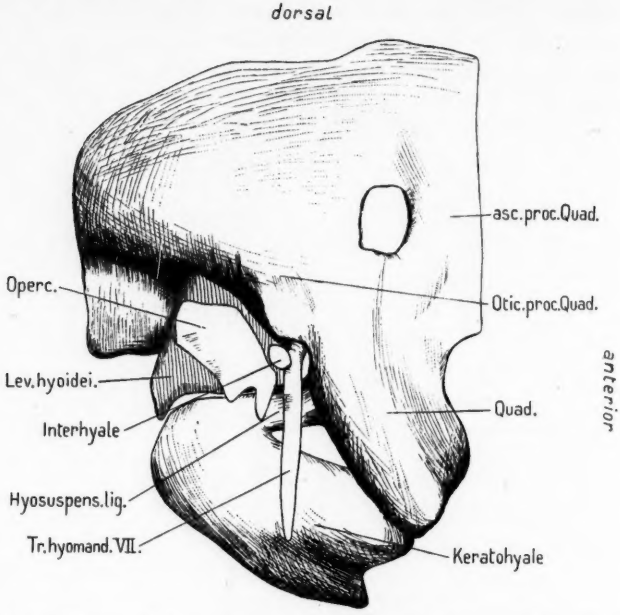

Fig. 22. *Ceratodus.* Embryo, 20 mm., drawing of model of Levator hyoidei, etc., antero-lateral aspect.

In support of his theory de Beer draws the following contrasts between Selachii and Teleostomi. "In Selachii the hyomandibular articulates with the auditory capsule halfway between the notochord and the lateral edge of the capsule. External to it, originating from the edge of the capsule is the hyomandibular muscle, and between the latter and the hyomandibular passes the lateralis vein." "In Teleostomes the hyomandibular articulates with the auditory capsule right at its lateral edge. Median to it is the hyomandibular muscle and the two veins, secondary and lateralis."

I doubt whether any one of these statements is a general truth, either in the case of Selachii or in that of Teleostomi.

First, as regards the position of the head of the hyomandibula relative to the auditory capsule. Though in *Scyllium* it abuts against the floor, yet

Gegenbaur, in 1872, showed that in *Heptanchus*, *Hexanchus* and *Mustelus*, the head of the hyomandibula abuts against the lateral surface of the auditory capsule about its middle, and that in *Acanthias*, *Perinodon*, *Galeus*, *Squatina*, *Scymnus* and *Centrophorus* it abuts against the lower part of the lateral surface of the auditory capsule. The head fits into a socket ("Pfanne"), but there is no true joint, and attachment is effected by a strong, but loose, ligament

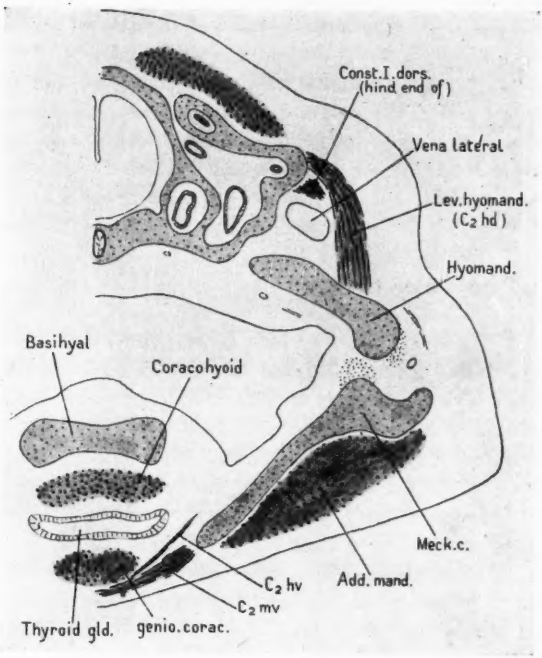

Fig. 23. *Mustelus canis*. Embryo 57 mm., transverse section.

("Band"). In *Cestracion* the hyomandibula abuts against the junction of the lateral and ventral surfaces of the capsule. White stated that in Laemargus the hyomandibula articulates with the lateral wall of the skull by two heads—anterior and posterior.

There is thus no constancy of position of the head of the hyomandibula relative to the auditory capsule. It may abut against its ventral surface, at the junction of ventral and lateral surfaces, at the lower part of the lateral surface, or higher up on it.

There is a similar variation in Teleostomi. The hyomandibula of *Salmo* abuts against the ventral surface of the auditory capsule (*vide* fig. given by Gaupp). In *Acipenser* (figs. 9–12) and *Lepidosteus* (fig. 18) it abuts against

the outer part of the ventral surface; in *Gasterosteus* (*vide* Swinnerton) against the junction of the ventral and lateral surfaces; in *Amia*, *Polypterus* (fig. 13), and *Polyodon* (*vide* Bridge) against the lateral surface.

I take it that by the term "hyomandibular muscle" of Selachii de Beer means that portion of the hyoid constrictor which is inserted into the hyomandibula and was first described, though not named, by Vetter and later termed "C_2hd" by Ruge and by Luther, and "levator hyomandibularis" by Tiesing and by Allis.

In Selachii, generally, the dorsal portion of the hyoid Constrictor spreads forwards as a continuous sheet, the fibres next in front of the dorso-ventral ones are inserted into the hyomandibula (C_2hd), and the most anterior ones into the hinder part of the palato-quadrate (C_2md). In *Chlamydoselachus*, *Odontaspis*, and *Scyllorhinus* (as depicted by Luther) there is only a C_2hd—no fibres being inserted into the palato-quadrate.

Now, no one of these authors describes or depicts the C_2hd as external to the hyomandibula. The muscle is dorsal to it. The fibres pass downwards, or downwards and slightly forwards, to the cartilage. The only case I know of in which fibres are stated to be external to the hyomandibula is *Acanthias vulgaris*, where, as described by Marion, the fibres next behind C_2md pass over the hyomandibula and are inserted into the keratohyale. Vetter, however, had stated that the fibres are inserted into the hyomandibula.

C_2hd does not always arise from the edge of the auditory capsule in Selachii—its origin varies in relation to that of the head of the hyomandibula. Thus in *Mustelus canis* (fig. 23) where the hyomandibula abuts against the lateral surface of the capsule, C_2hd arises from the lateral surface, and not from the edge, of the capsule.

I would here diverge for a moment to consider the special conditions in *Heptanchus* and *Hexanchus*. The hyomandibula lies external to the palato-quadrate, and the fibres next in front of the dorso-ventral ones are inserted into the palato-quadrate. C_2hd lies internal to it. It is probable, then, that C_2hd of these two Selachii is delaminated from the inner surface of C_2md, and is not homologous with C_2hd of other Selachii. In support of this theory it may be remarked that in a 70 mm. embryo of *Heptanchus* C_2hd is not yet developed (figs. 2 and 3). A new name might be given to it.

Ruge stated that in *Mustelus laevis* also the fibres of the Constrictor hyoideus inserted into the hyomandibula lie internal to those inserted into the posterior part of the palato-quadrate, i.e. that a condition exists which is similar to that of Hexanchus and Heptanchus. This however is not characteristic of the genus, for in a 57 mm. embryo of *Mustelus canis* (fig. 23), where the hyomandibula is posterior to the palato-quadrate, the most anterior fibres of the Constrictor hyoideus are inserted into the hyomandibula, and none into the palato-quadrate. The condition is thus similar to that described by Tiesing in the adult stage of *Mustelus laevis*. Neither Ruge nor Tiesing stated the relations of the hyomandibula to the

palato-quadrate. Possibly Ruge dissected some species in which the hyomandibula, or at least its upper part, lay internal to the palato-quadrate.

Though the Adductor hyomandibularis of *Polypterus*, *Amia*, *Lepidosteus*, and Telostei, is medial to the hyomandibula, yet its homologue the Retractor hyomandibulae of *Acipenser* and *Polyodon* is dorsal to the hyomandibula. It arises from the lateral surface of the auditory capsule, and passes downwards or downwards and slightly backwards to the hyomandibula (*vide* the descriptions and figures of Vetter and Danforth and fig. 7).

Though the lateralis vein is external to the hyomandibula in *Scyllium*, this relationship is not constant in Selachii. Thus the vein is dorso-external to the cartilage in *Acanthias* and *Mustelus* (fig. 23), and dorsal to it in *Heptanchus* (figs. 2 and 3). Though there are two veins medial to the hyomandibula in *Amia*, this number is not constant in Teleostomi. Thus in *Acipenser* (figs. 4–12) and in *Polypterus* there is only one—the v. jugularis of Schmalhausen and Allis.

de Beer's generalisations have thus been made from insufficient data.

CONCLUSIONS

1. The above observations show, I think, that the hyomandibula of Teleostomi is a single structure and not the result of fusion of two skeletal structures. When, as in most Teleostomi, there is a foramen for the passage of the tr. hyomandibularis vii, this is due to the skeletal element—primarily situated only anterior to the nerve—spreading backwards. When, as in some Teleostomi, the hyomandibula has two articular heads, this is due to a gradual development of the primary single articular head into two heads, and is not due to the fusion of any extra cartilage.

The next question is whether the hyomandibula of Teleostomi is homologous with that of Selachii. In favour of this homology are the following facts: (1) in both groups the hyoid bar is at first a continuous one, its upper end at first not reaching the auditory capsule and subsequently doing so; (2) the hyomandibula is the segmented-off upper part of this bar; (3) it comes into relationship with the auditory capsule—with any part of its floor or lateral surface, in both groups; (4) the relations of the muscle C_2hd to the hyomandibula in Chondrostei are similar to those in Selachii, i.e. it forms a Levator hyomandibulae.

The curious condition which arises in *Ceratodus* as a result of separation of the epihyale into portions is almost certainly a secondary one. It suggests that Dipnoi are descended from ancestors possessing a simple epihyale which passed from the keratohyale upwards and inwards beneath the auditory capsule. Such a structure is similar to, and probably homologous with, the hyomandibula of *Scyllium* and *Acipenser*. This suggests that Dipnoi, Selachii and Teleostomi are descended from common ancestors possessing a hyomandibula of this form and relationship to the auditory capsule. It would follow that the various other relationships of the hyomandibula to the auditory

capsule which occur in Selachii and Teleostomi are secondary conditions which have been independently acquired in these groups.

2. In Selachii and Ganoids C_2hd is inserted into the hyomandibula, whereas the Levator hyoidei of Dipnoi is inserted into the keratohyale. In view of the fact that the epihyale of *Ceratodus* does not persist as such, and is not developed in *Lepidosiren* and *Protopterus*, it is probable that the insertion of the Levator hyoidei into the keratohyale in Dipnoi is a secondary condition, and that Ruge was right in thinking the muscle homologous with C_2hd of Selachii and Ganoids, and giving it the same name. Further, in favour of this is the fact that in each group the muscle is formed by separation of the upper projecting part of the anterior edge of the Constrictor hyoideus[1].

The primary form of C_2hd was probably a muscle which, arising from the auditory capsule, passed downwards, or downwards and forwards, and was inserted into the hyomandibula and acted as a Levator hyomandibulae. This condition is preserved in Selachii and Chondrostei. Its position in *Polypterus*, *Amia*, and *Lepidosteus*, internal to the hyomandibula and its function as an Adductor, are probably secondary. In Teleostei the muscle-sheet spreads forwards to the palato-quadrate.

3. The tr. hyomandibularis vii has different relations to the hyomandibula in *Ceratodus*, Selachii and Teleostomi. In *Ceratodus* it passes anterior to it, in Selachii it passes downwards external to it, in Teleostomi it passes behind or through it. Examination of an early stage of *Scyllium* (fig. 1) shows that the tr. hyomandibularis vii passes outwards in front of the upper end of the (unsegmented) hyoid bar and then curves downwards external to it. There is thus a 2 : 1 probability that the primary relationship of the nerve to the hyomandibula is anterior, and that the condition in Teleostomi is a secondary one. The condition in *Polypterus*—where the r. mandibularis of the tr. hyomandibularis vii passes in front, and its r. hyoideus behind—may be regarded as an intermediate one.

I wish to express my thanks to Professor Swinnerton for embryos of *Gasterosteus*, to Miss Cross for the drawings of the models, and to Mr Emery, laboratory steward, for help in making them.

[1] The early form of the hyoid muscle-plate in *Amia* is shown in figs. 26 and 27, of a paper on "The Autostylism of Dipnoi and Amphibia" published in this *Journal* in vol. LIX.

Dec. 18, 1924.

ABBREVIATIONS

Add. hyomand.	Adductor hyomandibulae.
Add. mand.	Adductor mandibulae.
Asc. proc. Quad.	Ascending process of quadrate.
Art. carotis ext.	Arteria carotis externa (of Schmalhausen).
Aud. caps.	Auditory capsule.
Constr. I dors.	Constrictor i dorsalis.
Constr. II dors.	Constrictor ii dorsalis.
C_2md.	Portion of Constrictor hyoideus inserted into palato or pterygo-quadrate (Ruge).

Dil. operc.	Dilatator operculi.
dors. aorta	Dorsal aorta.
Geniobranch.	Genio-branchialis (-Branchiomandibularis of Vetter).
g. genie. VII.	Ganglion geniculatum vii.
hyoid. m. pl.	Hyoid muscle plate.
Hyomand.	Hyomandibula.
hyosuspens. lig.	Hyosuspensorial ligament.
jugular c.	Jugular canal.
Lev. hyoid.	Levator hyoidei.
mand. m. pl.	Mandibular muscle plate.
N. bucc. VII.	Nervus buccalis vii.
N. ophth. V.	Nervus ophthalmicus v.
N. ophth. VII.	Nervus ophthalmicus vii.
otic proc. Quad.	Otic process of quad.
Pal. quad.	Palato-quadrate.
Protract. hyomand.	Protractor hyomandibulae.
Retract. hyomand.	Retractor hyomandibulae.
Tr. hyomand. VII.	Tr. hyomandibularis vii.
V. cap. lat.	Vena capitis lateralis.
V. jugularis.	Vena jugularis.

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VALVES IN THE SPLENIC AND MESENTERIC VEINS OF THE SHEEP

By K. J. FRANKLIN, B.M., M.A.

AND

NOTES ON THE HISTOLOGY OF CERTAIN VEINS OF THE SHEEP

By F. HAYNES, B.A.

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THE following anatomical observations arose out of an investigation of the physiology and pharmacology of the isolated vein ring (1), (2), and are put on record here for three reasons.

The first is that we have been unable to discover any unequivocal statement as to the valves in the large mesenteric veins. Hochstetter (3) describes valves in the splenic veins in Carnivora and Ruminants, including, apparently, the sheep. Bryant (4) describes valves in the branches of the venae breves of the intestine of Man. The second is that in books on histology there does not seem to be any detailed account of the structure of veins in particular species, and it may therefore be of interest to publish histological observations on the large veins of one herbivorous animal. These differ markedly in some cases from the usual text-book description, and in addition give the histology of the splenic and mesenteric valves. The third and last reason is that we believe that the anatomy is a necessary basis for a right understanding of variations in the physiology and pharmacology of the veins of different species, and most of the work on isolated rings referred to above has been done on the veins of the sheep.

Valves in Splenic Veins of the Sheep

Appendix I gives a detailed account of the findings in thirteen splenic veins. It will be seen that in all except one there was at least one set of valves which would appear to be capable of preventing regurgitation of blood. This one case is apparently quite abnormal, because in every splenic vein (about twenty altogether) examined since this first series, valves have been present. The stereoscopic photograph (Pl. I, fig. 1) shows a splenic vein with two sets of valves. The spleen itself is seen at the bottom of this photo. The valves are usually bi-, sometimes tri-, cuspid.

Valves in Mesenteric Veins of the Sheep

These are not so regularly found as is the case with the splenic veins, but they are of sufficiently frequent occurrence to make the obtaining of specimens fairly easy. What are found more commonly are white marks or ridges on the vein wall where valves have either atrophied, or else never properly developed. The stereoscopic photograph (Pl. I, fig. 2) shows these marks as well as valves. The valves here, as in the splenic veins, are either bi- or tri-cuspid. There are usually single valves over the entrance of tributary veins, and these are often found even in those cases where there are no valves in the main vein. The complete absence of valves in the main vein is a fairly frequent finding. Vein No. 10 is interesting, as there were seven sets of rudimentary or atrophied valves in a total length of 22·5 cm. All the veins examined were large mesenteric veins, not small ones near their origin in the intestinal wall, like those mentioned by Bryant (*v. supra*).

THE HISTOLOGY OF CERTAIN VEINS OF THE SHEEP

The veins examined were:

Superior vena cava (thoracic).
Inferior vena cava (thoracic).
Renal vein.
Mesenteric vein.
Splenic vein.
Facial vein.
Superficial limb vein.
External jugular vein.
Iliac vein.

With the exception of the iliac vein, and a second mesenteric vein, all the veins were from the same sheep, and were fixed about twenty minutes after the animal's throat was cut.

The tissues were fixed in mercuric chloride-formol solution, and were embedded in paraffin in the ordinary manner, save that benzene was employed as the clearing agent in order to minimise hardening of the tissues. The observations were made on sections 8μ thick. The sections were stained in Delafield's haematoxylin and eosin and in Weigert's elastin stain followed by Curtis's substitute for van Gieson.

Superior vena cava (thoracic). In the intima there are, beneath the endothelium, fine circular elastic fibres, collagen and circular smooth muscle fibres alternating in thin bands.

The media consists first of longitudinal smooth muscle bundles enveloped in collagen fibres mingled with fine elastic fibres, and, beyond this, collagen with coarse, mainly longitudinal, elastic fibres alternating with thin bands of circular smooth muscle.

In the adventitia there is a feltwork of loose collagen and elastic fibres.

Inferior vena cava (thoracic). The intima of this vein is similar to that of the superior vena cava, but the elastic tissue is very scanty and consists only of very fine fibres.

In the media there is a fairly thick layer of collagen alternating with coarse elastic fibres, which are mainly logitudinal. There is in this layer a considerable amount of elastic tissue. Beyond this is a thin layer of alternating circular muscle and collagen fibres containing a few longitudinal elastic fibres.

The adventitia is composed of collagen fibres with a very few ramifying elastic fibres. This coat is bounded by a thin layer of elastin, covered by endothelium.

Renal vein. The thin intima consists of endothelium resting on very delicate circular elastic fibres, beneath which is a very thin band of circular smooth muscle alternating with collagen fibres containing a very few extremely delicate elastic fibres.

The media contains numerous longitudinal smooth muscle bundles surrounded by collagen fibres among which are fine and coarse circular and longitudinal elastic fibres. This coat is almost entirely muscular.

The adventitia consists of loose connective tissue.

Mesenteric vein. The intima consists of an alternation of circular elastic fibres, collagen and circular muscle fibres.

Next to this there is, in the media, a fair amount of collagen, containing thick elastic fibres, the direction of which is mainly circular. Beyond this there is a considerable number of longitudinal muscle bundles surrounded by collagen and longitudinal elastic fibres.

In the adventitia there are a few fine elastic fibres ramifying among the collagen.

A second specimen of mesenteric vein contains valves, which are composed of collagen covered by endothelium. Immediately underlying the endothelium there is a very small amount of extremely delicate elastic tissue.

Splenic vein. The intima of this vein comprises fairly coarse circular elastic fibres resting on circular smooth muscle. Among the latter are interspersed very thin collagen layers containing fine, mainly circular, elastic fibres. This coat is largely muscular.

Most of the media is composed of bundles of longitudinal smooth muscle surrounded by a little collagen with some longitudinal elastic fibres, but between this layer and the intima is a thin layer of collagen containing many coarse elastic fibres, most of them circular.

The adventitia consists of fairly loose collagen fibres, containing some ramifying elastic fibres.

This specimen contains valves, which are composed of collagen, with a very small amount of extremely tenuous circular elastic tissue immediately beneath the endothelium.

Facial vein. The intima consists of fairly thick circular elastic fibres resting

on very thin alternating bands of circular smooth muscle and collagen fibres. These latter contain fine elastic fibres, mainly circular.

The media is composed largely of collagen, in which lie circular smooth muscle bands surrounded by elastic fibres. External to these are a few bundles of longitudinal smooth muscle.

The adventitia consists of looser collagen fibres than the media, and contains much less elastic tissue.

Superficial limb vein. Beneath the endothelium there is a band of circular elastic fibres resting on fine alternating bands of circular muscle and collagen, the latter containing fine longitudinal elastic fibres.

A fairly thick collagen coat, with many coarse elastic fibres, mainly circular, forms the media. In this coat there is hardly any muscle.

The adventitia is mainly composed of collagen, there being only a few fine elastic fibres.

External jugular vein. In the intima there is a delicate elastic layer resting on a very thin circular smooth muscle coat. Beneath this is a considerable amount of collagen containing a very few delicate elastic fibres.

The media consists of numerous longitudinal bundles of smooth muscle surrounded by collagen fibres containing a large number of coarse longitudinal and circular elastic fibres.

The collagen with its elastic tissue shades off into the more loosely knit adventitia.

Iliac vein. In the intima there is a band of fine circular elastic fibres resting on an alternation of circular smooth muscle and collagen mingled with fine circular elastic fibres.

The media mainly consists of collagen fibres, with a fair amount of coarse and fine longitudinal elastic tissue. There is some longitudinal smooth muscle.

The adventitia is not clearly marked off from the media, and consists of a feltwork of collagen and fine elastic fibres.

A single set of bicuspid valves has been found in the splenic vein of a calf, the only animal of this species at present examined. There were none in the corresponding mesenteric vein.

Our thanks are due to Mr W. Chesterman, of the Anatomical Department, Oxford, for the making of the stereoscopic photographs of valves in the splenic and mesenteric veins.

SUMMARY

Valves occur commonly in the splenic vein of the sheep, and less frequently in the mesenteric veins of the same animal. The differential histology of the large veins of the sheep is described.

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APPENDIX I

VALVES IN SPLENIC VEINS OF SHEEP

1. Two sets of bicuspid valves separated by 0·8 cm.
2. Two sets of bicuspid valves separated by 1·2 cm.
3. Two sets of tricuspid valves separated by 0·5 cm. in a piece of vein 4·4 cm. long.
4. Two sets of bicuspid valves separated by 1·2 cm. in a piece of vein 3·5 cm. long; the proximal efficient, the distal not so efficient: distal pair 1 cm. from the spleen.
5. Three sets of bicuspid valves: the most distal pair 1 cm. from the spleen and efficient, the next pair 1·2 cm. from the first, and the third pair 1·1 cm. more proximal, these two pairs not very efficient. The whole length of the piece of vein 4·5 cm.
6. Two sets of bicuspid valves separated by 1·4 cm. in a piece of vein 3 cm. long: the distal set 1 cm. from the spleen: one cusp of the distal set and both of the proximal set efficient.
7. Two sets of efficient bicuspid valves separated by 2·4 cm. in a piece of vein 5 cm. long: the distal set 1·4 cm. distal from the spleen.
8. Two sets of bicuspid valves separated by 2·3 cm. in a piece of vein 4·5 cm. long: the distal set 1·3 cm. from the spleen and not very efficient, the proximal set efficient.
9. One set of efficient bicuspid valves in a piece of vein 3·3 cm. long, and 2·7 cm from the spleen.
10. No valves in a piece of vein 4 cm. long.
11. Two sets of bicuspid valves separated by 0·5 cm. in a piece of vein 2·8 cm. long, the distal set 1·5 cm. from the spleen and very efficient, the proximal set not very efficient.
12. One set of efficient tricuspid valves 1·8 cm. from the spleen in a piece of vein 3·6 cm. long.
13. Two sets of efficient bicuspid valves separated by 1·5 cm. in a piece of vein 4 cm. long.

APPENDIX II

VALVES IN MESENTERIC VEINS OF SHEEP

1. Rudiments of four sets of bicuspid valves at about 2·5 cm. interval.
2. One set of tricuspid valves: rudiments of another set of tricuspid valves about 2 cm. distal to the first set: valves over E.T.V. (entrances of tributary veins).
3. No valves.
4. No valves.
5. Rudiments of two sets of bicuspid valves, 2·5 cm. apart.
6. Rudiments of one set of bicuspid: one set of tricuspid 5 cm. distal to the first set: rudiments of another set: valves over E.T.V.
7. No valves.
8. Rudiments of two sets of bicuspid valves about 2 cm. apart: valves over E.T.V.
9. One set of bicuspid in one mesenteric vein just distal to its junction with another mesenteric vein.
10. Rudiments of seven sets of valves, some bi-, some tri-cuspid, in a length of 22·5 cm.: valves over E.T.V.
11. Rudiments of three sets of valves (including one functioning cusp) in 18 cm.: valves over some E.T.V.
12. Rudiments of two sets of valves in 16 cm.
13. Rudiments of five sets of valves in 13 cm.

N.B. In this appendix the term "rudiments" is used to denote the presence of atrophied or incompletely developed valves.

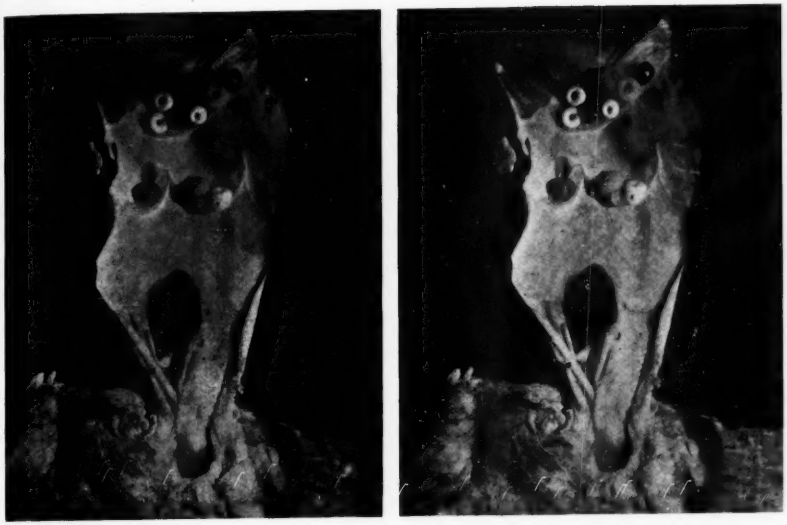

Fig. 1. Stereoscopic photograph of spleen and splenic vein (sheep) to show two sets of bicuspid valves. Three of the valves are loaded with beads. Width of vein at top: 24 mm.

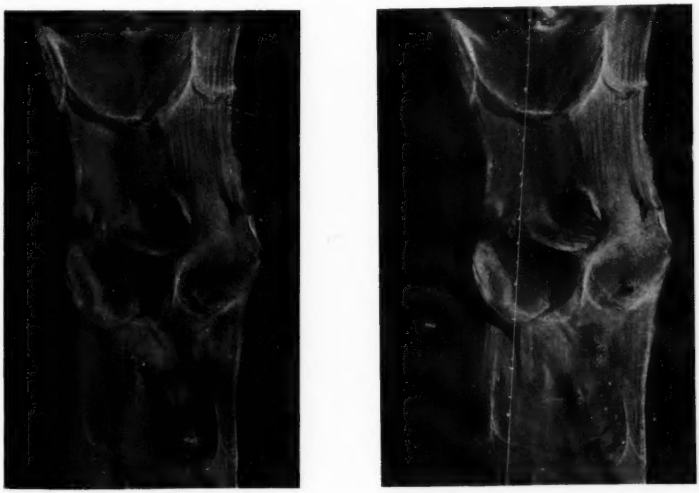

Fig. 2. Stereoscopic photograph of mesenteric vein (sheep) to show, from above downwards, a set of bicuspid valves, a valve over the entrance of a tributary vein, a second set of bicuspid valves, and an atrophied or imperfectly developed set of bicuspid valves. Width of vein at top: 21 mm.

ON THE ROTARY MOVEMENTS OF THE WRIST

By EDGAR F. CYRIAX, M.D. (Edin.),
London.

In the *Journal of Anatomy* for 1917 (LI, 396–399) I briefly referred to the fact that there is normally present a considerable amount of passive rotation of the wrist, but that no mention of this is to be found in anatomy books, though they always refer to the existence of passive rotation of the phalanges. I also stated that such rotation of the wrist can never be performed actively, only passively. Since writing the above, however, I have found out that the latter statement is in a way not strictly true, inasmuch as it is possible by means of a certain active movement of the forearm to bring about passive rotation of the wrist as one of its accompaniments.

This is performed as follows: the hand is placed flat on a table, preferably with the fingers abducted as this gives a wider base from which to ensure the subsequent immobility of the hand. The forearm may be held either horizontally or somewhat obliquely; keeping the hand quite still, alternate pronation and supination are performed: this induces passive rotation of the wrist first in one direction and then in the other. Fixation of the hand on the table by the other hand or by weights, etc., renders the movement easier of performance and increases its range.

In order to analyse the movement of wrist rotation into its component parts, I decided to try and estimate the movements of the individual carpal bones during such rotation. I accordingly made a series of investigations on about twenty arms, dissected as well as undissected, in the anatomy departments of St Mary's and Middlesex Hospitals, by kind permission of Professor Frazer and Professor Yates respectively, to whom I tender my best thanks, as I do also to Dr R. H. Robbins, prosector at the former hospital, for his help in the somewhat difficult task of locating the individual carpal bones in the undissected arms.

In order to make the estimations referred to, I employed a special apparatus of my own construction consisting essentially of two horizontal stages, one fixed and the other capable of being rotated about a horizontal axis, placed about $1\frac{1}{2}$ inches apart. By means of thumbscrews and strapping the forearm was firmly secured to the fixed stage, and the hand was fixed to the moveable one by means of thumbscrews applied over both distal and proximal portions of the metacarpals. A long pin was then driven from above into each carpal bone in turn. I placed myself so as to look along the forearm towards the elbow, and was enabled to read off the angle of each pin by means of a scale placed transversely in the interval between the two stages. The stage to which the hand was fixed was rotated as far as it would go alternately in opposite directions, the angle of the pins being read off in each case. The difference

between the two readings gave the amount of rotation of each carpal bone during the movements of maximum physiological rotation of the wrist.

The amounts of rotation of the wrist as a whole varied very considerably, especially in the undissected arms, in which readings as low as 11° and as high as 29° were encountered, the average being 19°. In the dissected arms the readings varied from 18° to 29°, the average being 24·5°. As regards the amounts of rotation in individual bones, considerable variations were also frequent, especially as regards the semilunar bone.

The following shows the average amount of rotation of each bone expressed in terms of the total amount of rotation of the wrist:

Scaphoid	54·5%	Trapezium	88·9%
Semilunar	55·5%	Trapezoid	89·8%
Cuneiform, Pisiform	72·0%	Os magnum	87·5%
		Unciform	92·2%

In the case of the last four bones the differences between their respective amounts of rotation and 100 must represent the rotation between them and the metacarpals.

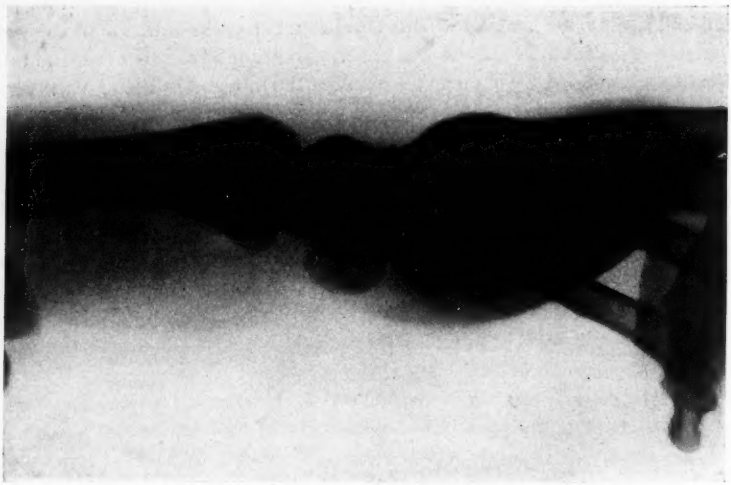

Fig. 1

In the living subject the range of passive rotation of the wrist as elicited by fixing the subject's radius and ulna with one hand and then rotating his hand alternately in both directions, is generally found to be about 45°, which is greatly in excess of the range obtained in the cadaver. This is because gliding movements in the antero-posterior plane of the metacarpals at their proximal ends supply an accessory factor in hand rotation and apparently increase the actual movement at the wrist joint. This can be demonstrated by the apparatus

mentioned above. If instead of firmly fixing both bases and heads of the metacarpals, only their heads are fixed with a force sufficient to prevent up and down movement *en masse*, but still permitting gliding movements of the bones at their proximal ends, the amount of rotation in the wrist is generally doubled. The result of this extra movement on the amount of rotation of the individual carpal bones is specially noticeable as regards the cuneiform (together with the pisiform) and the unciform (up to 30%) but much smaller in the other bones (up to 5%).

A number of skiagrams of the wrist during passive rotation were kindly taken for me by Dr Stanley Melville and Dr R. L. Rawlinson: in none of them was

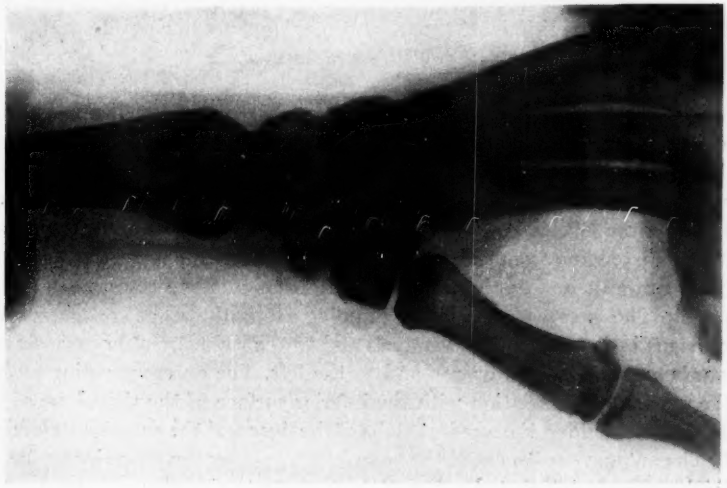

Fig. 2

it found possible to ensure complete immobility of the radius and ulna. The skiagrams reproduced herewith are those in which such movements were least. In them the change of position of the carpal bones are for the most part quite obvious, specially as regards the scaphoid and pisiform, as are also the accessory gliding movements of the metacarpals.

From the practical point of view, due recognition of the possibility of rotation in the wrist joint is important for the two chief reasons:

(1) The presence of the movement introduces a fallacy when testing for the range of pronation and supination as usually practised by rotating the patient's hand and forearm together, the elbow being fixed.

(2) When dealing with adhesions it is often very advantageous in order to break them down to apply movements that cannot be performed actively[1]. Passive wrist rotation will frequently accomplish what no other passive movement of the wrist can be got to do.

[1] See paper by the author and Dr Melville in the *New York Med. Journ.* 1921, CXIII, 538–540.

TRANSPOSITION OF ABDOMINAL VISCERA

By Professor N. PAN

Professor of Anatomy, Medical College, Calcutta

In an adult female subject brought into the dissecting room of the Medical College, Calcutta, during the winter term of 1923–4, transposition of some of the abdominal viscera was noticed. As such cases are comparatively rare and as pathological conditions of these transposed organs during life are apt to mislead the clinicians, I am publishing a short account of the peculiarities noted.

Gastro-intestinal Tract. The size of the stomach is small, being $7\frac{1}{2}$ inches in length and $2\frac{1}{2}$ inches in breadth. The cardiac orifice is situated at the level of the 11th thoracic vertebra on its right side. The left vagus nerve lies in front of and the right vagus nerve behind the cardiac orifice. The pyloric orifice is situated on the left side of the body of the 12th thoracic vertebra. The lesser curvature extending from the left margin of the oesophagus has the concavity directed upwards and to the left and gives attachment to the hepato-gastric ligament. The greater curvature extending from the right margin of the oesophagus is directed at first upwards and to the right, then downwards and forwards and finally downwards and to the left. The antero-superior surface of the stomach is in relation with the inferior surface of the right lobe of the liver, the gall bladder, the quadrate lobe of the liver and the anterior abdominal wall. The antrum cardiacum of the oesophagus grooves the posterior surface of the right lobe of the liver to the left of the fossa for the inferior vena cava.

Duodenum. The duodenum is horseshoe-shaped, with the convexity directed to the left. It is 4 inches in length and situated to the left side of the vertebral column, extending from the left side of the 12th thoracic vertebra to the left side of the body of the 2nd lumbar vertebra. The concavity of the duodenal curve embraces the head of the lower pancreas. The bile duct and the pancreatic ducts open separately on the postero-medial aspect of the duodenum, the opening of the bile duct lying half an inch lateral to the opening of the lower pancreatic duct. The hepato-duodenal ligament is attached to the commencement of the duodenum.

Jejunum and Ileum. The coils of the jejunum and the ileum are chiefly placed on the left side of the abdominal cavity. They measure only 9 feet in length.

Caecum. The caecum is situated in the lower part of the umbilical region on the right side of the middle line.

Ascending Colon. The ascending colon, 7 inches in length, passes upward and slightly lateralwards towards the spleen, lying in front of the upper limb

of the transverse colon and right kidney. The upper end of the ascending colon turns backwards and downwards forming the right colic flexure.

Transverse Colon. The transverse colon begins on the right side of the 2nd lumbar vertebra, passes towards the left in front of the 3rd lumbar vertebra and forms a bend on the left side of the body of the 4th lumbar vertebra. Then

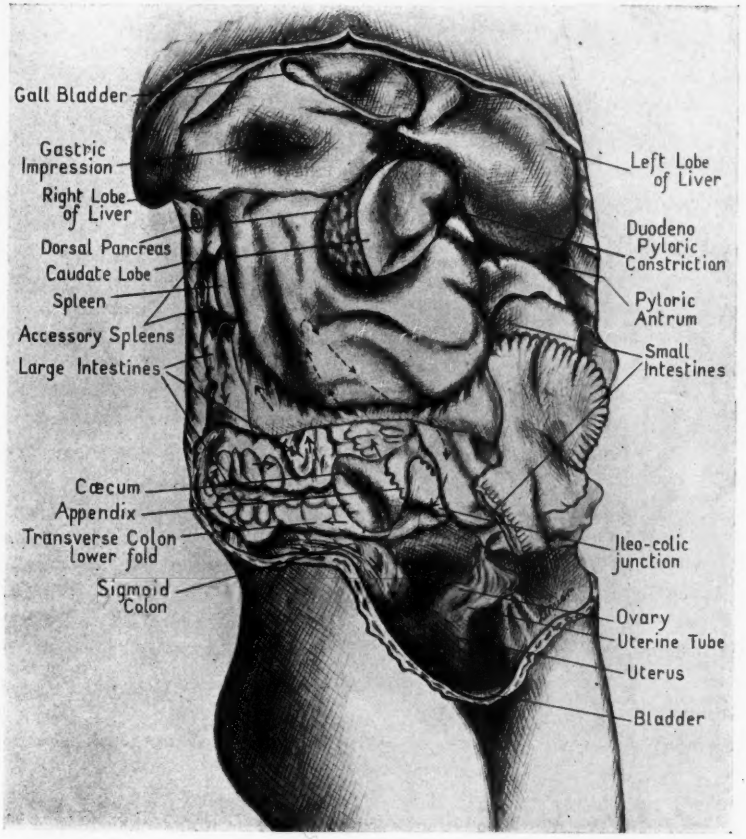

Fig. 1. Superficial View

it crosses the middle line to the right in front of the body of the 4th lumbar vertebra, lying below and parallel to the upper limb of the transverse colon. Then it passes upwards and to the right to form the splenic flexure. It has no mesocolon and its anterior surface lies under cover of the coils of the ileum, caecum and the ascending colon. The length of the transverse colon is 13 inches.

Descending Colon. It passes downwards and medialwards on the right side of the abdomen towards the ala of the sacrum. It measures 8 inches in length.

Sigmoid Colon. It is situated on the right side. It has no mesocolon. It measures 4 inches in length.

Liver. The caudate lobe is very prominent, measuring 2 inches by 1 inch by 1 inch. It hangs downwards in front of the vertebral column to the left side of the oesophagus above the lesser curvature of the stomach and the lower

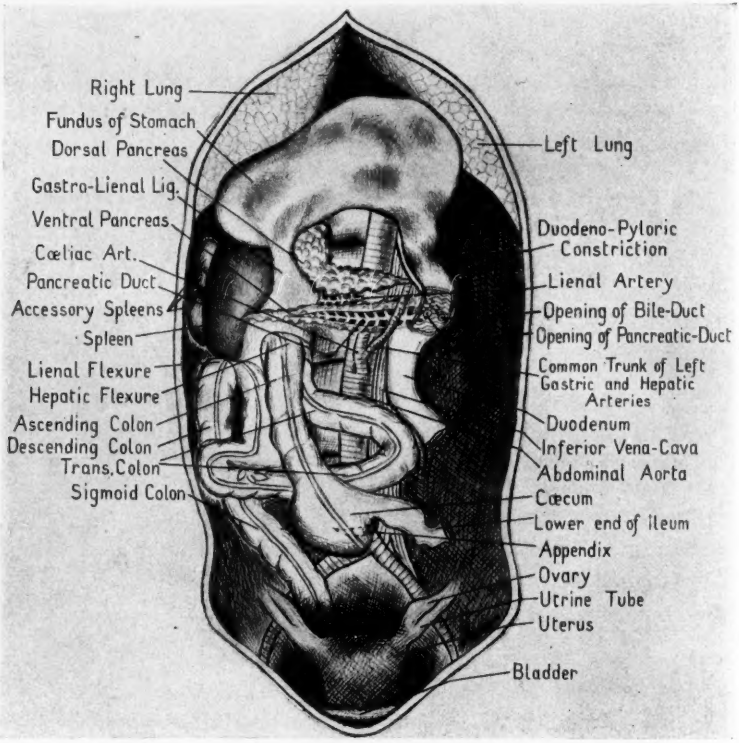

Fig. 2. Deep View, small intestines removed and stomach thrown upwards

pancreas but to the left of the upper pancreas. The inferior surface of the right lobe has the gastric impression but the splenic impression takes the place of the colic and renal impressions. The bare area is very small and the oesophageal impression lies on the posterior surface of the right lobe. The gall bladder lies in the cystic fossa in the right lateral line of the body. The inferior surface of the left lobe of the liver bears the renal impression for the left kidney.

Spleen. It is of a flattened oval shape and is situated in the right hypo-

chondriac region. Its anterior surface is in relation with the inferior surface of the right lobe of the liver, the postero-inferior surface of the stomach and the tail of the lower pancreas. The hilum occupies the lower fourth of the anterior surface near the right lateral border and is so deep as to subdivide partially the spleen into an anterior and a posterior portion. It looks downward and to the right and transmits the branches of the lienal vessels. The posterior surface of the spleen is in relation with the right suprarenal gland and the upper end of the right kidney, and the diaphragm separates it from the 10th and 11th ribs and the 9th and 10th intercostal spaces of the right side. The spleen measures 4 inches in length, 3 inches in breadth and 1½ inches in thickness.

Accessory Spleens. There are five accessory spleens, four being situated towards the upper end of the spleen and the fifth one at the lower end. They are all separate from the spleen and are contained between the two layers of the gastro-lienal ligament. Their sizes vary from ½ inch by ½ inch by ¼ inch to 1½ inches by 1 inch by ½ inch.

Pancreas. There are two pancreatic organs, an upper and a lower. The *upper pancreas* lies obliquely across the vertebral column passing from above downwards and to the left in the epigastric region. Its upper end is on the right side of the body of the 10th thoracic vertebra and its lower end is on the left side of the body of the 11th thoracic vertebra, where it lies in apposition with the head of the lower pancreas. It is prismatic in shape, the upper end being larger than the lower. It measures 3 inches by 1 inch by ½ inch. Its anterior surface is covered by the peritoneum of the omental bursa. Its posterior surface is uncovered by peritoneum. Its duct opens into the duodenum by a minute orifice separate from and above the orifices of the bile duct and the duct of the lower pancreas. It receives its blood supply from the pancreatic branches of the lienal artery, which arises directly from the front of the abdominal aorta above the origin of the coeliac artery, and passes towards the right below the upper pancreas.

The *lower pancreas* is larger than the upper pancreas. It measures 4 inches by 1 inch by ½ inch. It is also prismatic in shape. It is placed transversely across the vertebral column in front of the body of the 12th thoracic vertebra. A triangular interval separates its body and tail from the upper pancreas but its head is in close apposition with the lower end of the upper pancreas. It is covered anteriorly by peritoneum but uncovered posteriorly. It is supplied by branches derived from the lienal artery. Its duct begins near the tail on the right side and traverses its substance nearer to its posterior surface and then opens into the duodenum by a separate aperture unconnected with that of the bile duct.

The upper pancreas represents the dorsal pancreas which has failed to fuse with the lower one representing the ventral pancreas.

Abdominal Aorta. It lies in front of the vertebral column on the right side of the inferior vena cava. The following peculiarities are noted about its branches:

(1) The lienal artery arises separately and passes towards the right to the hilum of the spleen.

(2) The hepatic, left gastric and superior mesenteric arteries arise by a common trunk—representing the coeliac artery below the lower pancreas and the origin of the lienal artery.

(3) The inferior mesenteric artery passes towards the right.

(4) There are two renal arteries, in the left side of which the lower one passes to the lower end of the left kidney.

Inferior Vena Cava. It is formed by the union of the two common iliac veins in front of the body of the 5th lumbar vertebra behind the left common iliac artery. It ascends on the left side of the abdominal aorta and at the upper part of the abdomen slightly inclines forwards and to the right to reach the caval fossa on the posterior surface of the right lobe of the liver; on entering the thorax it opens into the right atrium. It receives the usual tributaries but the left ovarian vein opens into it direct and the right ovarian vein opens into the right renal vein.

Uterus and Ovaries. The uterus is retroverted. The ovaries and the fimbriated ends of the uterine tubes are situated in the iliac fossae above the back part of the brim of the pelvis.

There is no transposition of heart or lungs or of the large blood vessels of the thorax.

My thanks are due to Dr Bepin Behari Basak, Demonstrator of Anatomy, for carefully dissecting the abnormalities noted. I thank also Mr Dayanidhi Misra, student of the fourth year class of this College, for making the drawings for me.

ACTION OF X-RAYS UPON THE DEVELOPING CHICK EMBRYO

SERIES II & III

By HECTOR A. COLWELL, M.B., D.P.H.,
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In a preliminary communication entitled, "The action of repeated doses of X-rays upon the developing chick embryo," published in the *Journal of Anatomy*, October 1922, we came to the conclusion that, in chick embryos which were irradiated immediately before incubation and then subjected to daily irradiations for several days, the action was always inhibitory, the irradiated embryos being invariably smaller than the controls; and that *within the limit of radiation investigated* the effects seemed rather to depend upon the total amount of radiation reaching the embryos than upon variations in its quality or hardness. In this Series (Series I) all of which were irradiated immediately before incubation and on successive days during the earliest stages of development, of those which received a full pastille dose, six out of nine specimens examined showed no signs of development at all. In those in which development had taken place, with few exceptions, all the tissues and organs which should be normally developed during the period examined were differentiated but were smaller in size. There was thus diminution or retardation of growth, rather than an inhibition or arrest of the process of evolution of the different tissues and organs.

The present series of experiments (Series II and Series III) have been undertaken with the object of testing the effect of X-rays of different degrees of hardness on embryos which have been *allowed to develop normally for a period of 4 days before the commencement of irradiation.* They were then, in the case of *Series II*, subjected to daily doses of X-rays for a period of 3 days and were removed at the end of 7 days, the total period of incubation thus being 168 hours. In *Series III*, the incubation was continued for 8¾ days (210 hours), and the eggs were irradiated on each of the last 5 days of the incubation period. Accurate measurements of the "control" and "irradiated" embryos have been taken, and in Series II, the tables show that with the exception of those that were exposed to a full pastille dose, the average length was not markedly affected. Thus the length of two control embryos which were reserved for sectioning was in each case 7 mm., and the

average lengths irrespective of the effects of screening may be tabulated as shown below.

SERIES II. *Incubation 7 days (168 hours). Irradiation 3 successive days.*

Number of specimens (26)	Pastille dose P.D.	Average of greatest lengths mm.	Deviation from length of controls mm.
2	Controls	7	—
7	1	5·8	−1·2
9	$\frac{1}{2}$	7·1	+0·1
8	$\frac{1}{4}$	7	—

SERIES III. *Incubation* $8\frac{3}{4}$ *days (210 hours). Incubation without radiation,* $3\frac{3}{4}$ *days (90 hours). Incubation and irradiation, 5 successive days (120 hours).*

Number of specimens (26)	Pastille dose P.D.	Average of greatest lengths mm.	Deviation from length of controls mm.
2	Controls	17	—
6	1	18	+1
10	$\frac{1}{2}$	17·9	+0·9
8	$\frac{1}{4}$	17·9	+0·9

It will be noted that in Series III the average measurements show an increase in length of approximately 1 mm. in all three categories, as compared with the two control embryos. There seems however to be considerable range of variation in the length of normal chick embryos incubated for this period, the differences in length probably depending upon the breed, and upon variations in the degree of moisture and temperature of the air, and though each of the control embryos used in this series measured 17 mm. we have specimens of this age, and younger, which are considerably over 17 mm. in length. We hesitate therefore to conclude that the increase in length shown in this series is entirely due to a stimulating effect of the X-rays when applied at this period of development, as contrasted with the stunting influence when applied in the earlier stages of development.

The histological examination of the irradiated embryos has been carried out with the view of determining whether the X-rays have produced any visible effects upon the growing tissues or organs, and attention has been specially directed to the epithelium covering the surface of the body; the tissues of the central nervous system; the alimentary canal, and the organs developed from this tube; the blood; and the genital cells. Particular attention has also been given to the action of different degrees of hardness of the X-rays, and the embryos which have been selected for serial sectioning have been grouped in the following manner.

SERIES II. *Control.* (*Incubation 7 days.*)

Exposure to X-rays daily after 72 hours' normal incubation, until the time when the eggs were removed from the incubator (168 hours from the commencement of incubation).

Pastille dose		Thickness of aluminium filter	
P.D.		mm.	mm.
1	No filter	2	4
$\frac{1}{2}$	,,	2	4
$\frac{1}{4}$	,,	2	4

SERIES III. *Control.* (*Incubation* $8\frac{3}{4}$ *days.*)

Exposure to X-rays daily after 90 hours' normal incubation, until the time when the eggs were removed from incubator (210 hours from commencement of incubation).

Pastille dose		Thickness of aluminium filter		
P.D.		mm.	mm.	mm.
1	No filter	1	2	4
$\frac{1}{2}$	,,	1	2	4
$\frac{1}{4}$	,,	1	2	4

TECHNIQUE OF IRRADIATION

The apparatus employed was one of the ordinary coils used in the Therapeutic Department of King's College Hospital with a Coolidge tube. The current through the primary was about 4 amperes at a voltage of about 100 volts. The spark gap was about 6 inches and the anticathode was 4 inches away from the Sabourand pastille which was placed on the side of the filter away from the tube. The eggs were situated at a distance of 8 inches from the anticathode.

On opening the eggs the embryos were removed entire, all connections with the membranes having been severed; they were placed immediately in the following fixing solution:

Potassium bichromate	3 grms.
Glacial acetic acid	5 c.c.
Distilled water	100 c.c.

They were allowed to remain in this solution from 24 to 48 hours according to the size of the embryo. They were then washed in distilled water and placed in 50 % alcohol and subsequently passed through ascending grades of alcohol up to the absolute spirit. The specimens were then cleared in a mixture of alcohol and cedar wood oil. The entire embryo was then placed in a paraffin bath, and subsequently embedded in paraffin. They were afterwards stained on the slide with either (*a*) iron haemotoxylin and counter-stained with eosin, (*b*) Van Gieson, or (*c*) picro-indigo-carmine.

The preparation and staining of the serial sections were carried out by Mr J. Weston, and the authors wish to express their thanks to him for the excellent way in which he accomplished this part of the work.

The whole series were carefully examined under a high power of the microscope and when necessary with an oil immersion lens.

SERIES II

Surface Ectoderm

Control. The cutaneous ectoderm is already differentiated into a superficial stratum consisting of a single layer of flattened cells, the epitrichium, and a deeper layer of cubical, columnar, or polygonal cells. The number of cells in the deeper layer vary according to position; in certain situations being 3 or 4 deep, in others where growth is rapid, or the epithelium covers a delicate mesenchyme, e.g. over the cerebral vesicles, it consists of a single layer of flattened cells, and there is as yet no differentiation of an epitrichium. The cells of the deeper layer are frequently distended with a clear, unstained, mucinoid fluid. Karyokinetic figures are frequent and are well defined. Except occasionally as the result of accident, there is no separation of the cutaneous ectoderm from the underlying mesoderm.

1 *P.D. No filter.* The nuclei of the ectodermal cells are not so clearly defined as in the control, and the cytoplasm is not so transparent. The clear "nascent" hyaloplasm, or endoplasm around the nucleus is not so sharply marked off from the granular ectoplasm. The epithelium is separated in places from the underlying mesoderm; this condition however is sometimes present in the control. An epitrichial stratum is present in situations where the ectoderm is thickest, such as the dorso-lateral region over the mesodermic segments. In some places this is frayed out and separated from the underlying, or deeper stratum of the ectoderm.

1 *P.D.* 2 *mm. F.* The cells of the superficial stratum of the cutaneous ectoderm have the same appearance as in the preceding specimen. Mitotic figures appear to be about equally numerous with those seen in the control and the previous specimen, but appear less brightly stained.

The equator of the lens of the eye lies external to the margin of the optic cup, whereas in the control it is completely within the cup, and the optic vesicles are also considerably smaller than in the control and the cell outlines are less distinct.

1 *P.D.* 4 *mm. F.* The epidermis is separated in places from the mesoderm. The nuclei of the ectodermal cells take the stain well, and where mitosis is taking place, the chromosomes are distinct.

$\frac{1}{2}$ *P.D. No filter.* The superficial epidermal layer is separated in places. Mitoses are frequent.

The nuclei are stained fairly well.

$\frac{1}{2}$ *P.D.* 2 *mm. F.* The superficial epidermal layer is separated in places but not so markedly as in the previous unscreened specimen. The cell bodies are somewhat granular. Mitoses appear to be equally frequent with those in the control and preceding specimen.

$\frac{1}{2}$ *P.D.* 4 *mm. F.* The cells in general do not appear to differ from those of the control, but a few loose epitrichial cells, which are either unstained,

or very slightly stained, are seen on the surface. Some of the cells appear distended with a clear translucent fluid.

$\frac{1}{4}$ *P.D. No filter.* The epidermal cells are in places detached from the underlying mesoderm. They vary considerably in size and shape; some being flattened, others spherical or oval. The cytoplasm in places is albuminous in appearance, and is either unstained, or feebly stained.

$\frac{1}{4}$ *P.D.* 1 *mm. F.* The surface ectoderm does not appear to differ from the control. In some of the dividing nuclei, the chromosomes are very clearly defined, and do not appear to be altered in any way.

$\frac{1}{4}$ *P.D.* 2 *mm. F.* Similar to the preceding.

$\frac{1}{4}$ *P.D.* 4 *mm. F.* No change.

Neural Ectoderm

Control. The tissues of the neural tube present the usual histological picture of embryos at this stage of development. The central canal of the spinal cord, the ventricles of the brain, and the cavity of the primary optic vesicle, contain no free cells, and no blood corpuscles. The mesoderm surrounding the spinal cord and brain is in most places in direct relation with the external limiting membrane and contains numerous capillary blood vessels, and blood spaces filled with red blood corpuscles, in different stages of development.

1 *P.D. No filter.* The cell elements of the spinal cord are less clearly differentiated than those of the control; the cytoplasm being granular and slightly opaque in the irradiated specimen, more homogeneous and translucent in the latter. This difference is especially noticeable in the outer or reticular zone of the spinal cord. In the nuclei the chromatin is not so sharply demarcated from the karyoplasm, and where division is taking place the chromosomes appear clumped together in dense irregular masses. The number of nuclei undergoing mitosis appears to be about the same as in the control, there being no evidence of either increase due to stimulation or of decrease due to arrest. The same remarks apply to the neural wall of the brain and optic vesicle; proliferation, although it appears to be extremely active in the germinal layer of the cerebral wall and retina, is not more so than in the control.

1 *P.D.* 2 *mm. F.* The cell elements of the neural wall of the brain and spinal cord are well stained, but the cytoplasm is more granular and opaque than in the control; it is not so much affected however in this respect as in the unscreened specimen. In the epencephalon (cerebellum) there is a localised area, where an irregular cell proliferation has taken place, and neither the internal nor the external limiting membrane is recognisable as a definite stratum. The mitotic figures in this place also are not limited to the germinal zone but extend a considerable distance into the middle or nuclear zone. Many cells in the nuclear zone appear to be undergoing division by amitosis (*v.* Entoderm).

In the retina the external limiting membrane (internal limiting membrane of the adult organ) is detached in places and thrown into irregular folds. The pigment layer shows an irregular distribution of the pigment granules, and opacity of the cytoplasm. A few blood corpuscles are present in the cavity of the secondary optic vesicle, and in the vicinity of the choroidal fissure.

The epithelium of the optic vesicle, and the cells of the spinal, acusticofacial and Gasserian ganglia were examined and compared with the control and unscreened specimens, the general cell picture being found to be similar to that of the neural walls and retina.

1 *P.D.* 4 *mm. F.* The germinal cells of the spinal cord and brain show frequent mitotic figures, which do not differ in any noticeable manner from those in the control. In some instances however, especially in the retina, the chromosomes appear to be "clumped" and not so well defined as in the normal. In the outer layer of the secondary optic vesicle, pigment is present in normal amount, and the granules are discrete.

$\frac{1}{2}$ *P.D. No filter.* The microscopic appearances are not quite so well defined as in the control.

The mitotic figures are about equally frequent. No free cells are seen in either the central canal of the spinal cord, or in the ventricles of the brain. The cell picture of the retina is very similar to the preceding specimens. The pigment granules in the outer or ensheathing layer of the optic cup are well defined.

$\frac{1}{2}$ *P.D.* 2 *mm. F.* The trabeculae of the neurosyncytium are not so clearly defined as in the control. Mitotic figures are frequent. A granular fibrinous material is deposited on the inner or vitreous surface of the retina, and the cell elements are irregular in their disposition, as compared with the even radial arrangement of these which is present in the control.

$\frac{1}{2}$ *P.D.* 4 *mm. F.* The cell elements are fairly well defined, and numerous nuclei are seen in the germinal layer undergoing mitosis. Pigment granules are present in the outer layer of the retina but are not very sharply defined.

$\frac{1}{4}$ *P.D. No filter.* The general appearance of the cell elements of the wall of the neural tube and optic vesicles is not much altered. The chromatic material of the dividing nuclei is however clumped together in masses, so that it is difficult to recognise the individual chromosomes.

$\frac{1}{4}$ *P.D.* 1 *mm. F.*, 2 *mm. F., and* 4 *mm. F.* No perceptible alteration from the normal, in either the neural syncytium or retina.

Entoderm

1 *P.D. No filter.* The entodermal cells lining the alimentary canal and pulmonary tracts are not so well defined as in the control, though their nuclei are distinct, and numerous cells are undergoing mitosis. The same remarks apply to the secretory epithelium of the liver and pancreas. In the former however small groups of deeply stained, shrunken and irregular nuclei are occasionally present, near the walls of the hepatic sinuses, and have the

appearance of having been injured by a direct and localised action of the X-rays.

1 *P.D.* 2 *mm. F.* The entoderm of the pharyngeal region of the foregut shows numerous nuclei in different stages of mitosis, and also groups of cells, with small nuclei, having one, sometimes two, well-defined nucleoli. They appear to have arisen by amitotic division, as in the elongated oval nuclei which exhibit two nucleoli, there is frequently a constriction in the nuclear membrane, indicating the site of a future division line. In some this division line is complete, and the two halves of the parent nucleus and cell are hemispherical; while in others two daughter cells of small type lie close together. These appearances are not confined to the entodermal cells of this specimen but are present in the control, and other irradiated specimens, and are probably normal. The nuclei resemble very closely those of the cell elements in the mantle layer of the neural tube.

1 *P.D.* 4 *mm. F.* The epithelial cells lining the alimentary canal do not appear to be altered to any appreciable extent. Mitotic figures are present and the chromosomes are well defined. The cells of the hepatic cylinders do not appear much affected. In some however the distribution of the secretory granules is irregular, parts of the cell body being clear, and others crowded with granules. The granules are seen most distinctly in the specimens stained with eosin.

$\frac{1}{2}$ *P.D. No filter.* The epithelium lining the alimentary and respiratory tracts is not much altered. There is no separation of the cells from the basement membrane. The nuclei are well defined, though the cell outlines are not easily recognised. A few yolk cells are seen in the lumen of the gut, which appear to be undergoing absorption.

$\frac{1}{2}$ *P.D.* 2 *mm. F.* The appearances are similar to those in the preceding specimen.

$\frac{1}{2}$ *P.D.* 4 *mm. F.* The entodermal cells lining the alimentary tract are in certain places detached from the underlying mesoderm. The cytoplasm appears to be somewhat more opaque and more granular than in the control. The secretory cells of the liver also appear somewhat cloudy, otherwise they do not differ from those of the control.

$\frac{1}{4}$ *P.D. No filter.* The cells lining the alimentary and respiratory tracts do not appear to be altered, some near the central lumen of the alimentary canal appear to be undergoing mucoid changes.

$\frac{1}{4}$ *P.D.* 1 *mm. F.*, 2 *mm. F.*, 4 *mm. F.* No appreciable alteration can be detected in either the lining epithelium of the alimentary tract or secretory cells.

Mesoderm

No definite changes could be detected in the coelomic mesothelium, or in the lining epithelium of the vessel walls in any of the irradiated specimens.

The mesenchyme also appears normal, and differs very markedly from that of the specimens described in our preliminary communication which

were irradiated from the commencement of incubation, and in which the mesenchymal tissues appeared as an irregular network of fibrin-like strands, with sparsely scattered and poorly stained nuclei, at the nodes. In these specimens moreover there were few blood vessels or blood spaces, whereas in the present series these are numerous and, as compared with the controls, contain an approximately equal number of blood corpuscles. The sub-endothelial tissue in the 1 P.D. unscreened specimen in the region of the endocardial cushions and "bulbis cordis" is torn in places, possibly as a result of the fixation process, but otherwise no very definite lesions could be detected.

The Blood

Control. The blood of a normal 7-day chick embryo contains a large proportion of erythrocytes which have attained their full size, and which

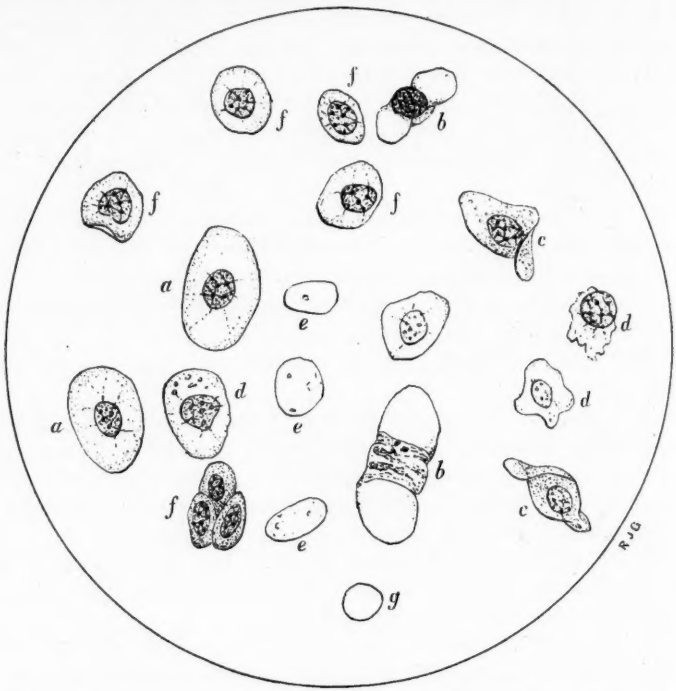

Fig. 1. Types of erythrocytes, drawn with a camera lucida, at an equal magnification, from the blood of an irradiated chick embryo, incubated 9 days.

a. Two fully developed normal erythrocytes. *b.* Type of distorted erythrocyte frequently present in the control specimens as well as in the irradiated. *c.* Erythrocytes showing various degrees of folding and twisting of the cell body. *d.* Degenerated corpuscles. *e.* Non-nucleated elliptical plates. *f.* Immature erythrocytes. *g.* Hyaline disc.

Obj. 1/12 in. Oil immersion. C.O. × 8

differ only from those of the 9-day chick embryos described in Series III (fig. 1), in having a more rounded form, and containing larger and more numerous eosinophil granules, so that in specimens stained with haematoxylin and eosin, their cell bodies have a pinkish tinge; whereas in the 9-day embryos, Series III, the cells are more flattened, the cytoplasm is less granular, and it has a yellow tinge. In the 7-day embryos there are a considerable number of rounded immature forms, and very occasionally an erythrocyte in a vessel or endothelial lined space may be seen in one or other stage of mitosis. Non-nucleated blood cells are frequently seen, and also red blood cells with pale, feebly stained nuclei. These will be described in greater detail in Series III.

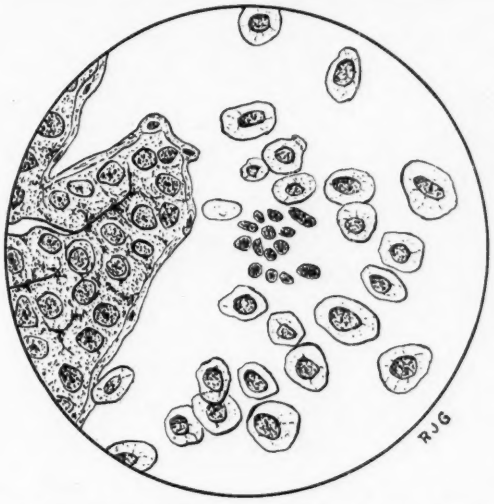

Fig. 2. Section through part of an hepatic cylinder, and an adjoining hepatic sinus, showing a group of microcytes, surrounded by erythrocytes and one non-nucleated blood corpuscle, from a control specimen, incubated 9 days.
Obj. 1/8 in. Apochrom. C.O. × 8.

Microcytes or primitive lymphocytes are occasionally seen in groups, either in the general blood stream, in the sub-endothelial tissue of vessels or in endothelial lined spaces in the dorsal region of the thorax (figs. 2 and 3).

1 *P.D. No filter.* The erythrocytes are frequently irregular in outline, and fragmented; sometimes small agglutinated masses of broken up blood corpuscles are seen. In place of the regularly disposed, discrete eosinophil granules of the cytoreticulum which are characteristic of the normal cell, in certain cells of the irradiated specimens the coloration is diffuse.

1 *P.D.* 2 *mm. F.* The outlines of the red blood cells are frequently irregular, and sometimes the cell bodies are fissured. The granules of the cytoreticulum are irregularly distributed, and appear to vary more in size than

they do in the control, but the diffuse coloration mentioned as occurring in some of the broken-up erythrocytes in the unscreened specimen is not seen in this specimen.

1 *P.D.* 4 *mm. F.* The same appearances are present in this specimen as in the preceding. A few lymphocytes are visible within the blood vessels.

½ *P.D. No filter.* A fair proportion of the nuclei of the red blood corpuscles are feebly stained or are not stained at all. In some no nucleus is visible. Lymphocytes are occasionally seen, but are few in number.

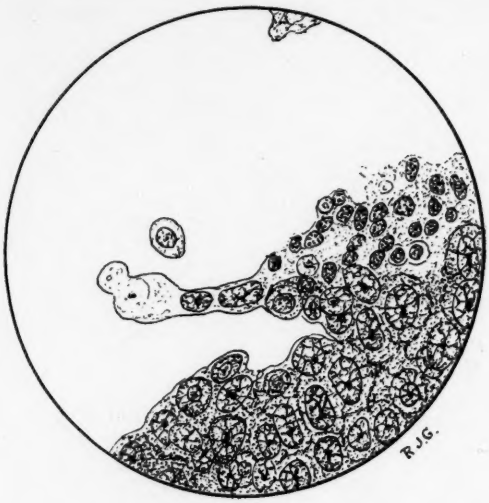

Fig. 3. Section through a process projecting into an endothelial lined space, situated to the left of the thoracic aorta and at the level of the root of the left lung. A group of oval or spherical nuclei is seen in the sub-endothelial tissue. The endothelium lining the vessel has disappeared in this situation, rendering it possible for the group of nuclei, with the surrounding protoplasm, to become shed off into the lumen of the vessel, where the nuclei, surrounded by a thin covering of protoplasm, would become separated and appear as a group of microcytes or primitive lymphocytes. The section is from an irradiated chick embryo, incubated 7 days, ½ P.D., 4 mm. F., but similar appearances are present in the control specimens, and the proliferation of the nuclei must not be regarded as due to any stimulating action of the X-rays.

½ *P.D.* 2 *mm. F.* The general appearance of the blood corpuscles resembles the preceding unscreened specimen, a few cells are fragmented, and some do not contain a nucleus.

½ *P.D.* 4 *mm. F.* Many of the red blood corpuscles are irregular in outline and they differ considerably in size, some appear swollen and are almost spherical in outline, others are shrivelled and have granular contents. The nucleus in many cells is imperfectly stained, and in others seems to have disappeared altogether. A few free nuclei are present.

$\frac{1}{4}$ ***P.D.*** ***No filter.*** The blood picture is very similar to the preceding series, and does not differ markedly from the control. A few free blood corpuscles are present in the mesenchyme surrounding the neural tube. Some red blood corpuscles are seen to contain no nucleus, while in others but very occasionally extrusion of nuclei seems to be taking place. The majority of the non-nucleated coloured discs however exhibit no sign of any central cavity or passage leading from such to the surface, and it seems probable that the nucleus has disappeared by absorption and not by extrusion. A few small cells with spherical nuclei which stain deeply with haematoxylin are present in the capillary blood vessels; some of these with only a small covering of cytoplasm and spherical in outline appear to be lymphocytes; others which are oval or spindle-shaped resemble the cells described by Jolly as "fusiform blood-cells" and by some authors as thrombocytes owing to their supposed action in the coagulation of the blood. Both types of cells are present in the control as well as in other of the irradiated specimens. They do not appear to be affected either in number or in any other way by the strength of X-rays employed in these series.

$\frac{1}{4}$ ***P.D.*** ***2 mm. F.***, and $\frac{1}{4}$ ***P.D.*** ***4 mm. F.*** No appreciable alteration could be detected in either of these specimens.

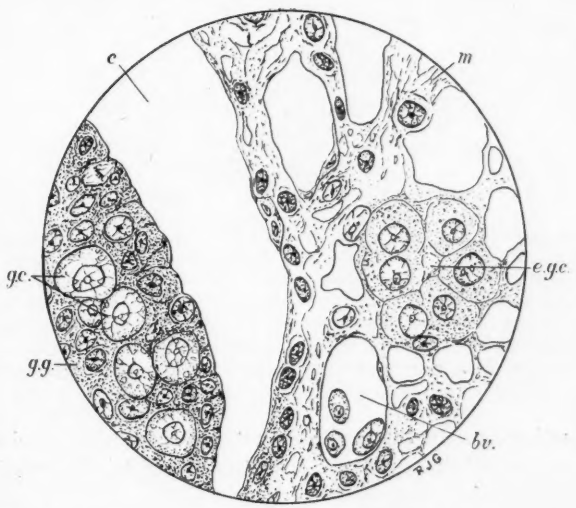

Fig. 4. Section through the genital gland, and adjacent portion of the mesentery of a chick embryo incubated 9 days, showing a multinuclear "extra-regional" genital cell in the root of the mesentery, and "regional" cells in the genital gland. Cell outlines are visible in the extra-regional cell, but the separation of the cell-elements is incomplete.

B.V. Blood vessel containing erythrocytes. *c.* Coelom. *e.g.c.* Extra-regional genital cell. *g.c.* Regional cells. *g.g.* Genital gland. *m.* Mesentery.

Control specimen. Camera lucida drawing $\times 750$ D. Obj. 1/8 in. Apochrom. C.O. $\times 8$.

Urogenital System

Control. Both the mesonephroi and the genital glands are well advanced in their development. We have directed our attention specially to the condition of the "primary" and "secondary" genital cells (figs. 4, 5 and 6). Several single and multinuclear primary genital cells, termed by some authors the "extra-regional" or "wandering" cells are present in the mesentery near the upper end of the urogenital ridge. They have the usual granular character of the cytoplasm, and large vesicular nuclei with wide-meshed, delicate,

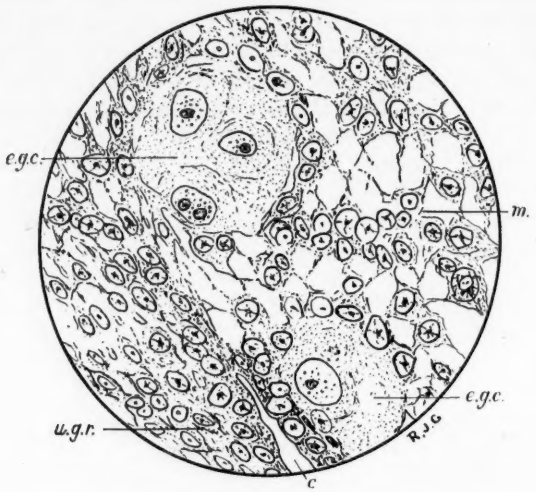

Fig. 5. Section passing through the angle where the root of the mesentery becomes continuous with the urogenital ridge, in an irradiated chick embryo incubated 7 days. Two multinuclear "extra-regional" genital cells are seen in the root of the mesentery. The cell outlines are indistinct, and the cytoplasm has become fibrillar. Two nucleoli are seen in the nucleus of one of the cell elements in the larger multinuclear cell. The cytoplasm of both genital cells is directly continuous with that of the surrounding mesenchyme.

c. Coelomic cavity. *e.g.c.* Extra-genital cells. *m.* Mesentery. *u.g.r.* Urogenital ridge. 1 P.D. No filter. Slide 4.

chromatin reticulum. In the genital gland, a considerable number of what appear to be transitional forms between the "secondary" genital cells and the coelomic epithelium are present.

1 *P.D. No filter.* The epithelium lining the Wolffian tubules and ducts does not appear to have been appreciably affected. Mitotic figures are present and the cell nuclei are well defined. Several single and multinuclear "extra-regional" genital cells are present in the mesoderm at the root of the mesentery. In one of the multinuclear cells, a nucleus which is much larger than the others appears to be degenerating.

1 *P.D.* 2 *mm. F.* No definite changes can be detected in the epithelium lining the mesonephric tubules or Wolffian duct.

1 *P.D.* 4 *mm. F.* The cells lining the Wolffian tubules appear uniformly granular, and few vacuoles are present, there is no sign of any destructive action of the X-rays, such as detachment of the epithelium.

½ *P.D. No filter.* A few tubules of the Wolffian bodies contain blood corpuscles in their lumina, and there is some irregularity in the disposition of the epithelial cells.

½ *P.D.* 2 *mm. F.* The genital cells on the surface of the gonad, and in the

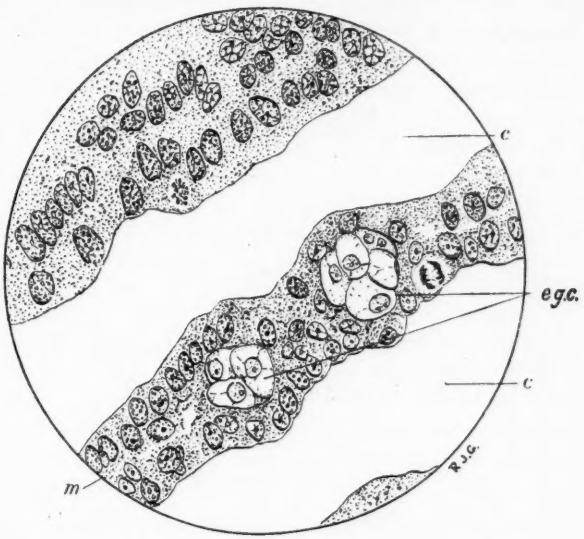

Fig. 6. Section through the mesentery of an irradiated chick embryo, incubated 9 days, showing two groups of "extra-regional" genital cells. The cell outlines are distinct, and the cytoplasm clear and albuminous in appearance. In one cell what appears to be an amitotic division of the nucleus is unaccompanied by any constriction of the cell body.
c. Coelomic cavity. *e.g.c.* Extra-regional genital cells. *m.* Mesentery.
½ P.D. 4 mm. Filter. Slide 2.

cortical layer beneath, do not show any appreciable deviation from the normal. In the sub-endodermal tissue of the allantois are some large cells which resemble the extra-regional genital cells found in the mesentery. Some of these cells have a clear translucent cytoplasm, others are filled with refractile granules (yolk). They do not appear to be affected by the irradiation.

½ *P.D.* 4 *mm. F.* Secretory cells of Wolffian body are well defined, and do not appear in any way affected.

¼ *P.D. No filter.* Large single, and multinuclear "extra-regional" genital

cells are present in the mesentery opposite the urogenital ridge. Some of these show the ordinary protobroque nucleus (*v.* Winniwarter), in others degenerative changes are visible both in the nucleus and cytoplasm.

$\frac{1}{4}$ *P.D.* 2 *mm. F.* No changes.

$\frac{1}{4}$ *P.D.* 4 *mm. F.* A few "wandering cells" are present in the mesentery. They do not appear to be affected by the irradiation.

Amnion

The amnion does not appear to have been greatly affected by the irradiation. In the specimen subjected to 1 *P.D.* 4 mm. F., however, both the ectodermal and mesodermal layers of the amnion appear irregular, and in some places are fused together; and the same condition is noted in the specimen $\frac{1}{2}$ P.D. 2 mm. F., and the nuclei and chromatic material are stated to be less defined than in the control.

SERIES III

Total period of incubation: $8\frac{3}{4}$ days (210 hours).

Incubation without irradiation: $3\frac{3}{4}$ days (90 hours).

Incubation with irradiation applied successively for the last 5 days (120 hours) of the total period.

Controls average 17 mm. in length.

Cutaneous Ectoderm

Control. The superficial stratum of the cutaneous ectoderm or epitrichium consists of a single layer of large flattened cells, underneath which is a layer of rounded or columnar cells arranged with their long axes at right angles to the surface. Neither superficial nor deep cells stain readily with any of the stains employed. The cytoplasm is slightly granular; the nuclei are well defined, although not deeply stained; karyokinetic figures are infrequent; the chromosomes in these are usually well defined. Feather-follicles are beginning to develop and appear as slight elevations of the ectoderm lying over thickened areas of condensed mesoderm. The epitrichial stratum, or the whole layer of cutaneous ectoderm, is occasionally separated from the deeper layers. This separation however is infrequent, and where it does occur, it is possibly the result of manipulation.

1 *P.D. No filter.* The epitrichium is detached in many places, and in some extensively. The cell outlines generally are blurred, especially those of the epitrichial stratum. Karyokinetic figures are present, but infrequent as in the control. The chromosomes do not appear to be so well defined as in the

control, there is however little difference in the number or size of the granules in the cytoplasm and there appears to be no alteration in the degree of development of the feather-follicles.

1 *P.D.* 1 *mm. F.* There is no noticeable change in the cutaneous ectoderm of this specimen, which resembles very closely the control.

1 *P.D.* 2 *mm. F.* The epitrichium is much separated and in places is broken. In some places also there is cleavage between the epidermis and the underlying dermis. The changes in the cell outlines and nuclei are similar to, though not so marked, as in the following specimen, 1 P.D. 4 mm.

1 *P.D.* 4 *mm. F.* In this specimen there is only slight evidence of detachment of the epithelium. The cell outlines and nuclear figures in the dividing cells are not so well defined as in the control.

Neural Ectoderm

Control. The cells and nerve-fibres forming the tissues of the central nervous system, including the retina, are brightly stained, and the histological picture is well defined. The ventricles, central canal of the spinal cord, and cavities of the primary optic vesicles, contain no free cells. The ventricles contain the usual irregular network of fine fibrils deposited from the cerebrospinal fluid. The cells of the outer or ensheathing layer of the optic cups contain well-defined pigment granules, situated in a clear protoplasm. The nuclei, when not obscured by the pigment, appear as clear oval areas devoid of granules.

1 *P.D. No filter.* The cells and nerve fibres of the neural ectoderm are not so well defined as in the control, and the chromosomes of the dividing nuclei are often clumped together in masses. In one situation the internal limiting membrane lining the central canal of the spinal cord is ruptured, and the lumen of the canal is partially filled with a fibrinous-like deposit containing a group of small oval cells derived from the neuro-syncytium forming the wall of the injured tube. The pigment cells of the retina are not so clear as in the control. The pigment granules are not so evenly distributed, and the cytoplasm is diffusely stained with pigment so that the nuclei of the cells are difficult to recognise.

1 *P.D.* 1 *mm. F.* The cells generally are somewhat clearer than in the preceding specimen.

1 *P.D.* 2 *mm. F.* Similar changes to those observed in the 1 P.D. no filter.

1 *P.D.* 4 *mm. F.* The histological picture does not differ in any notable way from the specimen treated with the unfiltered rays, if anything the defects are somewhat greater. Karyokinetic figures do not appear to be either more or less frequent than in the control.

Mesoderm

1 *P.D. No filter.* The denser masses of mesoderm such as those in the limbs and branchial arches do not appear appreciably affected; the more open mesenchyme around the optic vesicles and neural tube appears more fibrous and the tissue spaces more irregular than in the control.

1 *P.D.* 1 *mm. F.* Sub-cutaneous vessels in dorsal region distended with blood corpuscles, and appear somewhat larger, and more numerous than in the control.

1 *P.D.* 2 *mm., and* 1 *P.D.* 4 *mm. F.* No distinctive changes.

Genito-urinary System

Control. Genital cells are frequently seen in the epithelium covering the surface of the genital gland and in the cortical layer beneath this. They may be easily recognised by their large size; spherical outline; clear albuminous looking cytoplasm, and large spherical nucleus, the "germinal vesicle." The nuclear membrane is well defined and the chromatic material of the resting nucleus is in the form of a wide-meshed network of fine intersecting filaments radiating from the nucleolus. The germinal cells frequently appear in groups of 3 or 4, and in some cases a single germinal cell may possess two or more nuclei. Karyokinetic figures are occasionally seen but are infrequent. In the mesentery, and in the mesoderm adjacent to the genital gland, single or large multinucleated cells of the same type as the cells in the genital gland are sometimes seen. These are known as the "extra-genital" or "wandering" cells, and are believed to migrate from the yolk sac to the genital gland (figs. 4 and 6). Some of the large multinuclear cells show signs of degeneration such as fibrillation or vacuolation of the cytoplasm and loss of their capacity to absorb the staining material (fig. 5). In one of these, which was situated in the mesentery, there were as many as nine nuclei. They give the impression of cells in which the completion of the normal process of division, by constriction of the cytoplasm and separation of the daughter cells, has been arrested owing to deficient vitality of the cell element; and further, that owing to the direct continuity of their cytoplasm by strong protoplasmic strands with the surrounding mesoderm they would be incapable of migration and would not reach the ovary, but perish *in situ.*

Another point of importance to be considered in the comparison of irradiated with control specimens is that the normal process of degeneration of the mesonephros, which takes place at this period of development, is already far advanced in the latter, and that these normal degenerative processes may readily be attributed to the direct or indirect action of the X-rays. The degenerative changes seen in the mesonephros consist of: vacuolation and subsequent disintegration of the cytoplasm of the secretory cells; shrinking

and irregularity in the shape of their nuclei; imperfect staining reaction, and separation of the epithelial cells from the basement membrane, the cells afterwards becoming completely detached and shed off into the lumina of the tubules. Moreover the blood vessels become greatly enlarged and distended with corpuscles, and haemorrhages into the intertubular tissue and into the tubules themselves are of frequent occurrence. Any record in embryos which have been exposed to X-rays of what appear to be destructive lesions of the mesonephros must therefore be considered from the standpoint of a possible augmentation or acceleration of the normal degenerative processes, and not as an account of lesions which are produced solely by the irradiation.

1 *P.D. No filter.* The mesonephros shows signs of degeneration, with extensive haemorrhages. There is marked vacuolation of the secretory cells, many of which have not taken the stain well, or have remained unstained. Scattered groups of erythrocytes are present in the stroma of the ovary. A few germinal cells exhibit karyokinetic figures.

1 *P.D.* 1 *mm., and* 1 *P.D.* 2 *mm.* The intertubular spaces of the mesonephros are packed with blood corpuscles, and the lumina of the tubules are filled with a muco-fibrinous material. The germinal cells vary greatly in size, and the chromatic material is irregular in appearance.

1 *P.D.* 4 *mm.* Similar changes are present in the mesonephros of this specimen to those which we have noted in the preceding and in the unscreened specimens. A few groups of blood corpuscles are visible on the surface of the genital gland; others are seen in the substance of the organ either in the stroma, or in endothelial lined spaces.

Blood

Control. A circumstance which is of great interest from the biological standpoint is that many of the blood corpuscles from the 7th day of incubation onward show signs of degeneration. Erythrocytes are seen which are irregular in form, have shrunken nuclei, and fissured or disintegrated cytoplasm. Their cell bodies do not stain well, with either eosin or picro-carmine, and the chromatic material of the nucleus, instead of showing the usual deep purple colour, is only feebly stained with haematoxylin. In some cells the nucleus has completely disappeared, and the cell body remains as a pale ellipsoidal plate, which is commonly about half the size of a fully developed erythrocyte, and is sometimes fragmented. These cells are frequently seen in the intertubular tissue of the degenerating mesonephros, in the hepatic sinuses, in the principal blood channels through the cavities of the heart, and in the main blood vessels; whereas the small capillary blood vessels, and spaces in the mesenchyme, contain a large proportion of small, rounded, immature erythrocytes, or erythroblasts, and few if any degenerating cells.

It is possible that some of these degenerating blood cells arise in the mesonephroi, where considerable haemorrhages into the intertubular connective tissue and into the lumina of the tubules takes place at this stage of development. The blood in these spaces, having left the general circulation, will be in a condition of stasis, and thus may participate in the degeneration of the organ as a whole. Should any of this blood be re-absorbed into the general circulation, the condition which is described above may be explained without assuming that the duration of life of any individual blood cell of the embryo is an extremely short one.

These non-nucleated elliptical plates are however almost equally frequent in the 7-day control and irradiated specimens in which degeneration of the mesonephros is not so advanced, and it is possible that they may have some other origin than that suggested.

It is probable moreover that during the life of an adult individual, degeneration of a certain number of the blood corpuscles is constantly taking place, and that this condition of some of the blood cells may be attributed to disease. It is obvious also that any investigation of the effects of X-rays upon embryonic blood is rendered more difficult by the presence of degenerating cells in the circulation of the normal embryo. It may be assumed however that the effects of irradiation on the blood would be general rather than local, and it is probable that the action on the blood corpuscles would be by means of alterations in the physical or chemical constitution of the plasma rather than a direct action on a limited number of the blood corpuscles themselves.

1 *P.D. No filter.* Great irregularity is present in the size and shape of the erythrocytes, and the nuclei frequently appear shrunken and are in general deeply stained so that the structure of the nucleus is obscured. A considerable number of the cells are devoid of a nucleus. Groups of lymphocytes are occasionally present, but are infrequent. A small number of "fusiform cells" (Jolly) are present either in groups or singly. Their cytoplasm is more deeply stained with eosin than that of the erythrocytes and is accumulated chiefly at the two poles of the spindle. They appear to be derived from the endothelium lining the hepatic sinuses and other blood spaces.

1 *P.D.* 1 *mm. F.* The general appearance of the blood is like the preceding specimen. The vessels of the mesonephros are distended with corpuscles, and a few blood cells have escaped into the lumina of the tubules, and into the peritoneal cavity.

1 *P.D.* 2 *mm. F.* Large masses of granular fibrinous material which are almost devoid of corpuscles lie in the sinus venosus and extend downwards from this into the inferior vena cava and hepatic sinuses. The endothelial lining of these sinuses is detached in places from the epithelium of the hepatic cylinders. There is marked congestion and enlargement of the intertubular capillary vessels of the mesonephroi. The capillaries of the glomeruli are packed with immature erythrocytes. This condition, notwithstanding the

advanced state of degeneration of the organ, is present in the control and all the irradiated specimens.

1 *P.D.* 4 *mm. F.* Similar changes to those described in 1 P.D. 2 mm. were present in this specimen.

½ *P.D. No filter.* The blood corpuscles closely resemble those of the preceding series, all stages of degeneration being observable, and numerous non-nucleated ellipsoidal plates being present in the larger blood spaces. A group of 18 lymphocytes was noted in an endothelial lined space in the posterior mediastinum, similar to that portrayed in fig. 2. They apparently arise in the sub-endothelial layer of vascular spaces and are cast off in masses into the general circulation or lymphatic vessels (fig. 3).

½ *P.D.* 1 *mm.*, 2 *mm. and* 4 *mm. F.* No noticeable difference could be detected between the screened and unscreened specimens of this group.

¼ *P.D. No filter.* The erythrocytes vary much in size and shape. Many are shrunken and irregular in outline, with a shrunken, deeply stained nucleus. A considerable number of cells are destitute of a nucleus, or have a nucleus which is feebly stained, and in which the nuclear membrane is absent or ill-defined. Other cells show what appears to be an aborted karyokinetic figure, the chromatic material is massed in a spindle-shaped figure, with thick club-shaped processes running outward, but no signs of division of either the nucleus or cell body. These cells are present in all the specimens examined, including the control.

¼ *P.D.* 1 *mm. F.* Erythrocytes very irregular in shape and size, and their nuclei often much shrunken. Many blood corpuscles in the vessels of the yolk sac appear to be broken up and disintegrated.

¼ *P.D.* 2 *mm. F.* The secretory epithelium of the mesonephros does not appear to be so much affected as in the unscreened specimen, but there is a large quantity of blood in the vessels and spaces of the intertubular connective tissue.

¼ *P.D.* 4 *mm. F.* The erythrocytes vary in size and shape, and there is a considerable number of these cells which are destitute of a nucleus. They do not appear to be so much altered as in the unscreened specimen, or those of other series in which a stronger pastille dose has been administered.

Entoderm

The epithelium lining the alimentary canal, and that of structures which are developed as outgrowths from this canal, has been carefully examined throughout the series, and more particularly the cells lining the respiratory passages, and the secretory cells of the liver, and pancreas.

Control. The cells lining the alimentary tract are evenly arranged, their cytoplasm is finely granular, and they possess a clearly stained nucleus. The lumina of the bronchial tubes contain no free cells, and no mucoid material. The free borders of the lining epithelial cells, which are directed towards the

lumen, show a striated edge, indicating an early stage in the development of cilia. The liver cells are sharply outlined and the granules in the cytoplasm are distinct; they do not vary greatly in size, and are evenly distributed.

1 *P.D. No filter.* The entoderm lining the alimentary tract and air passages of the respiratory system does not appear much affected. Cilia are beginning to appear in the epithelium bounding the bays of the terminal bronchioles. These are not so clearly defined as in the control. The cell outlines of the hepatic cells are not so distinct as they should be, and where nuclei are undergoing division the chromosomes appear to be clumped together in masses. The granules of the cytoplasm are irregularly distributed, and vary considerably in size.

1 *P.D.* 1 *mm. F.* Appearances closely resemble the preceding specimen.

1 *P.D.* 2 *mm. F.* On examining the entoderm lining the bronchioles, it is observed that in some sections groups of detached nuclei with adherent masses of cytoplasm are lying inside the lumina of the tubules; these, and the adjacent cells, exhibit various stages of degeneration. The hepatic sinuses appear to contain a larger quantity of blood than is normal in embryos at this stage of development.

1 *P.D.* 4 *mm. F.* What appears to be inspissated mucus is present in the lumina of some of the bronchioles and air passages. The hepatic sinuses are very full of blood corpuscles. The hepatic cells show similar changes to those described in 1 P.D. no filter.

$\frac{1}{2}$ *P.D. No filter.* Localised areas of the liver tissue are present, where the liver cells are damaged and also the blood corpuscles in the hepatic sinuses. The erythrocytes are irregular in form, and in some places fragmented, or completely broken up. Some of the sinuses are filled with fibrinous material, while others are closely packed with blood corpuscles.

$\frac{1}{2}$ *P.D.* 1 *mm. F.* The epithelium lining the bronchioles and alimentary tract is not perceptibly affected, the cell outlines and chromosomes often being beautifully clear; and neither free cells nor mucus are present in the lumina of the tubules.

$\frac{1}{2}$ *P.D.* 2 *mm. F.* The entoderm lining the bronchioles and alimentary tract is not materially affected. The hepatic cells show irregularity in the deposition of the granules, and the nuclei are not so well stained as in the control. The blood cells in the hepatic sinuses are in some places very irregular in shape and size and the degree of staining of their nuclei is very variable, the nucleus sometimes being pale, and sometimes absent; small unstained oval and fusiform cells are occasionally seen.

$\frac{1}{2}$ *P.D.* 4 *mm. F.* The epithelium of the bronchioles and alimentary tract does not appear to be affected. Karyokinetic figures are frequently seen and are well defined. The hepatic cells show irregularity in the disposition of the granules, parts of the cell bodies being clear, other parts being crowded with granules. The endothelial cells lining the hepatic sinuses frequently appear

swollen, and in some places are shed off into the sinuses. A few lymphocytes are present in the sinuses, and also small unstained oval and fusiform cells.

$\frac{1}{4}$ *P.D. No filter.* The epithelium lining the alimentary tract and air passages is not perceptibly altered. The secretory epithelium of the liver and pancreas shows no definite lesions.

$\frac{1}{4}$ *P.D.* 1 *mm. F.* The free edges of the entodermal cells lining the bronchioles are seen to be irregular in places, but otherwise the lining epithelium of the alimentary tract and respiratory passages appears normal.

$\frac{1}{4}$ *P.D.* 2 *mm. F.* The free edges of the entodermal cells lining the alimentary canal and air passages show slight irregularities.

$\frac{1}{4}$ *P.D.* 4 *mm. F.* No definite injury to the epithelium is perceptible. The hepatic sinuses are closely packed with blood corpuscles.

CONCLUSIONS

A consideration of the detailed observations which we have made on the effects of the X-rays in Series II and Series III, shows that the principal action of the rays as revealed by the microscopic appearance of the tissues is destructive and is exerted chiefly on the cutaneous ectoderm; the neural tube and associated structures such as the retina and optic vesicle; the epithelium of glandular structures, e.g. the liver, or the mesonephros, and upon the red blood corpuscles. Moreover the action appears for the most part to be general rather than local, and probably becomes apparent some time after the irradiation rather than immediately after, as has been shown to be the case in the action of X-rays and radium radiations on the epidermis and subcutaneous tissues in the human subject, and on the cutaneous epithelium of amphibian larvae. The most pronounced changes occur in specimens which have been subjected to full pastille doses, and to unfiltered rays as contrasted with screened.

The ordinary signs of a reactive inflammation, such as a small round-celled infiltration, and fibrinous deposits, are not apparent in the growing tissues of the chick embryo at the stages dealt with in these series. Any local indication of the action of the X-rays in the strength, and for the periods which we have employed in these Series II and III, thus appears to be purely destructive, and consists in detachment of epithelium; diminution in the transparency of the cytoplasm, or the formation in the cytoplasm of minute granules or vacuoles; variations in the degree of distinctness with which the chromosomes may be distinguished in the dividing nuclei, and in the distinctness of the staining reactions of the nuclei and cell bodies. The effect of the X-rays on the blood corpuscles also appears to be purely destructive. In one or two cases a fibrinous clot almost destitute of corpuscles was observed in the heart or larger blood vessels, which suggests that there may have been a direct action by the X-rays on the plasma which will have altered its chemical

constitution and caused its coagulation. The appearances suggest that the action of the X-rays on the blood corpuscles may be partly indirect by inducing changes in the chemical constitution of the plasma, and partly direct upon the corpuscles themselves; and the same mode of action may be conceived to take place in the tissues of the body, which may be affected indirectly through the circulating tissue fluids and also by direct action of the rays upon the cell elements.

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THREE CASES OF RIGHT-SIDED SIGMOID COLON

By B. BHATTACHAYYA, M.B.

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During the winter session, 1923–4, three cases of right-sided sigmoid colon were found among 59 bodies dissected.

Case I

Adult male. Cause of death—pneumonia.

The caecum is situated above the right iliac crest, in front of the right kidney. The ascending colon is about 2½ inches in length. The transverse and descending colons are normally placed. In the left iliac fossa, the descending colon takes a sharp bend upwards towards the right, reaching the body of the 3rd lumbar vertebra. It crosses the middle line to the left of the mesentery and comes down to the right iliac fossa, where it becomes fixed to the posterior abdominal wall. From there the sigmoid colon goes down into the pelvic cavity, crossing the right brim of the pelvis and reaches the left side of the sacrum to end in the rectum. The meso-sigmoid is attached to the right side.

Case II

The subject is an old female. Cause of death—debility.

The caecum lies in the right iliac fossa. The ascending and the transverse colons are normally placed. The descending colon goes down to the left iliac crest and then crosses the middle line in front of the 4th lumbar vertebra. It then passes to the right iliac fossa behind the free end of the caecum. The sigmoid colon beginning on the fossa goes down into the pelvic cavity as in the previous case, by crossing the right pelvic brim.

Case III

The subject is an adult male. Cause of death—chronic nephritis.

The caecum lies in the right iliac fossa. The ascending and the transverse colons are normally situated. The descending colon comes down to the left iliac fossa where it is sharply folded upon itself and courses upwards to the right, crossing the middle line at the level of the 5th lumbar vertebra. It then reaches the right brim of the pelvis whence the sigmoid colon descends into the pelvic cavity. The meso-sigmoid is attached to the right side from the ilio-caecal junction to the middle of the sacrum.

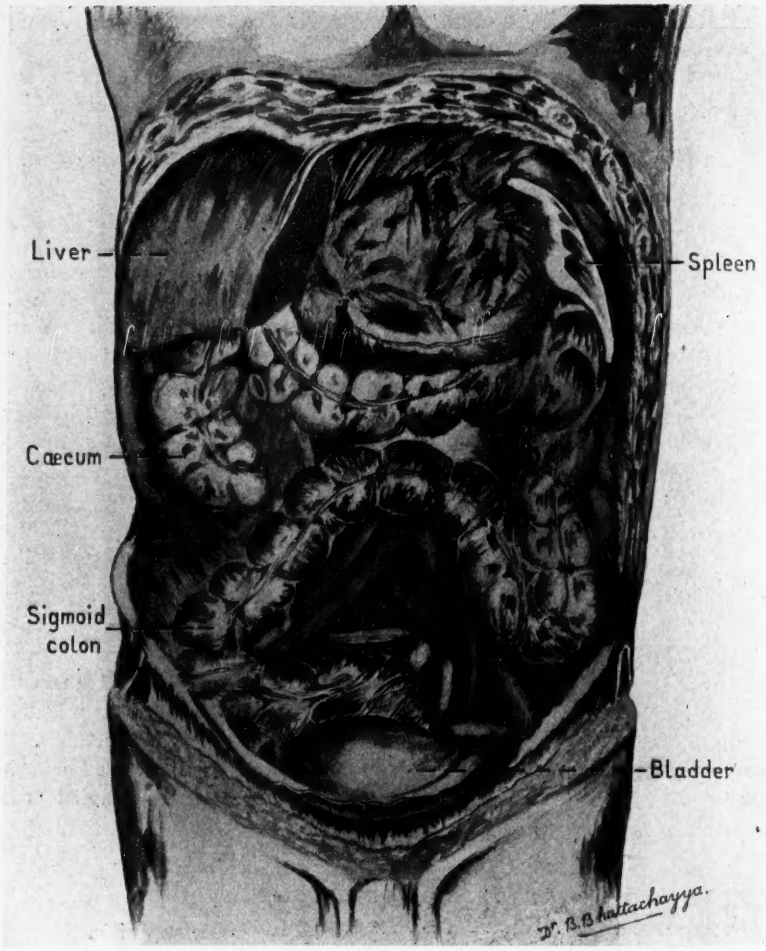

Fig. 1. Showing the arrangement of the sigmoid colon in Case I.

Fig. 2. Photograph of the arrangement of sigmoid described in Case II.

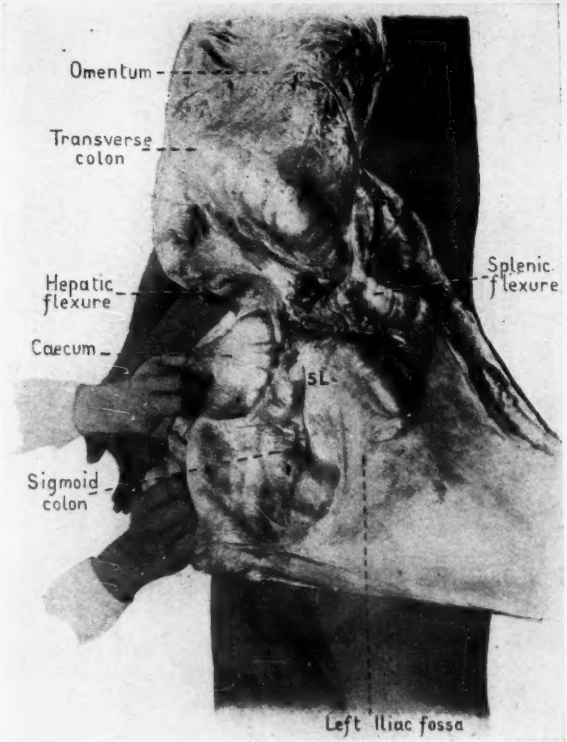

Fig. 3. The arrangement of parts described in Case III.

CONCLUSION

In each of these three cases, the total length of the colon was increased. The histories show that the causes of death in these cases are other than abdominal; nor were there any signs or symptoms pointing to intestinal trouble during life.

This abnormality is very difficult to explain. Probably there was secondary rotation of the large intestine while the primary rotation was taking place in the small intestine. This rare anomaly is interesting from a clinical point of view and may mislead the surgeons in various abdominal operations.

My best thanks are due to Prof. M. N. Bose, M.B., C.M. (Edin.), for kindly allowing me to publish these cases.

APPOINTMENT

THE Challis Chair of Anatomy in the University of Sydney, left vacant by the lamented death of Professor John Irvine Hunter, has now been filled by the election of Mr ARTHUR NEVILLE ST GEORGE HANDCOCK BURKITT, B.Sc., M.B., heretofore Associate Professor in the same Department.

Professor Burkitt had a distinguished career as a student, both in Science and in Medicine, in the University of Sydney. He obtained First Class Honours in Zoology under Professor Haswell in 1910 and graduated with First Class Honours in Science and in Medicine in 1916.

During the war he joined the Royal Australian Navy as a Medical Officer. Even during this period of service he continued to carry on biological research as opportunity permitted.

In 1919 Mr Burkitt decided to devote himself to scientific teaching and research, and on the nomination of Professor Wilson he was appointed as a Demonstrator of Anatomy.

After the appointment of Professor Hunter to the Challis Chair in 1922, Mr Burkitt was promoted as Associate Professor. He was soon given leave of absence by the Senate for purposes of overseas travel and study, and in pursuance of his programme he spent a year in acquiring familiarity with the activities of various anatomical schools both in Europe and America.

Professor Burkitt has specially interested himself in the problems of physical anthropology and has published several papers on the anatomy of the Australian aboriginal, in collaboration with Professor Hunter, Mr G. H. S. Lightoller and others. But he is also a promising worker in the fields of comparative anatomy and of embryology, as well as in histology, the teaching of which is now in the hands of the anatomical department in Sydney.

Professor Burkitt may be confidently relied on to maintain and extend the reputation of the school of which he is himself so distinguished a graduate.

L'ORIGINE DES CELLULES DU SANG DANS LE FOIE EMBRYONNAIRE DES MAMMIFÈRES

J. HAVET

University of Louvain.

L'ORIGINE des cellules du sang dans le foie embryonnaire des mammifères a fait l'objet de nombreux travaux.

L'un des derniers en date, celui d'un éminent hématologiste, le Professeur Jolly de Paris, arrive à la conclusion que cette origine est encore inconnue. L'auteur observe de "grosses cellules lymphoïdes" dont l'origine lui échappe; elles auraient traversé l'endothélium des vaisseaux du foie et elles se seraient insinuées entre les cellules hépatiques. Là, dans un milieu favorable, elles deviendraient la souche des cellules sanguines.

De nouvelles recherches sur ce sujet ne sont donc pas inutiles.

Celle que nous présentons ici éclaircira peut-être quelques points; si elle ne donne pas la conclusion définitive, elle attirera l'attention d'observateurs plus habiles sur un point assez important de nos connaissances d'embryologie.

Nous allons résumer brièvement les diverses opinions qui ont cours sur l'origine des cellules du sang dans le foie embryonnaire des mammifères.

1°. Les cellules endothéliales des vaisseaux seraient la source des cellules du sang dans le foie embryonnaire.

2°. Non seulement les cellules endothéliales, mais aussi les cellules du mésenchyme, leur donneraient naissance.

3°. Pour d'autres auteurs, des cellules du sang, préalablement formées dans une autre région, pénétreraient entre les cellules hépatiques, et se trouvant en un milieu favorable, ces cellules se multiplieraient et formeraient de nouvelles cellules sanguines.

Pour le Professeur Jolly, ce serait spécialement une grosse cellule lymphoïde qui s'introduirait entre les cellules du foie, et qui en se divisant donnerait naissance aux cellules sanguines.

4°. Les cellules du foie embryonnaire, c'est-à-dire, les cellules hépatiques, seraient l'origine des cellules sanguines. Janosik croit que les cellules du foie embryonnaire se diviseraient par voie directe, par amitose, et donneraient ainsi naissance aux cellules sanguines.

Aron[1] pense que les cellules du foie elles-mêmes, par une suite de transformations qu'il étudie longuement, deviennent des globules du sang.

La conclusion générale de cet auteur, c'est que dans le foie de l'embryon les cellules sanguines proviennent de la transformation des cellules hépatiques, éléments dérivés de l'endoderme. Il observe dans le foie embryonnaire des

[1] *Archives de morphologie générale et expérimentale*, 1922.

cellules claires et des cellules sombres, ainsi que de nombreuses formes de passage entre les deux types. Les cellules claires comme les cellules sombres peuvent se transformer en cellules sanguines. Des cellules hépatiques, naissent les cellules-mères correspondantes aux hémogonies de Mollier; elles deviennent indépendantes, elles se détachent du bourgeon hépatique, et elles poursuivent leur transformation en globules rouges ou hématies.

Ce sont surtout les changements qui surviennent dans le protoplasme que l'auteur étudie.

Quant au noyau des cellules hépatiques, il se borne à nous en dire, qu'il est devenu plus riche en chromatine, plus colorable par les colorants nucléaires.

L'étude du noyau nous paraît, au contraire, d'une très grande importance. Nous allons le montrer bientôt.

Janosik[1] dans un travail sur le développement des globules sanguins chez les Amniotes, étudie la formation des globules du sang dans le foie d'embryons de porc et d'opossum. Sans nous arrêter aux détails, donnons la conclusion qui concerne les mammifères: "les cellules hépatiques se divisent en petites cellules, lesquelles forment des ilôts. Les éléments des ilôts parviennent dans la circulation par déhiscence de l'endothélium des petits vaisseaux. Une fois en liberté (et quelques-uns même déjà dans les ilôts), plusieurs d'entr'eux se transforment en érythroblastes nucléés; le plus petit nombre nous fournit les leucocytes définitifs."

D'après Janosik la division des cellules du foie se ferait par voie directe.

Cette conclusion de l'auteur demanderait à s'appuyer sur des preuves suffisantes qui font défaut. D'ailleurs les dessins exécutés à un grossissement beaucoup trop faible n'apportent aucun appui à cette conclusion, qui ressemble à une affirmation gratuite.

Maximow[2] dans ses recherches sur le sang et sur le tissu conjonctif, donne un chapître qui traite des débuts de la formation du sang dans le foie.

L'auteur constate que cette question est loin d'être résolue, et que les opinions les plus diverses existent sur ce sujet. M. B. Schmidt[3], Lobenhoffer[4], Jost[5], Schridde[6] et d'autres, croient que les globules rouges naissent des cellules endothéliales des capillaires du foie. En se divisant, elles donneraient des cellules sanguines à l'intérieur des vaisseaux et à l'extérieur. Saxer met aussi en jeu le mésenchyme voisin des capillaires. Ce mésenchyme donnerait naissance à ses "primären Wanderzellen." De celles-ci naîtraient les globules rouges et les globules blancs.

[1] Janosik. "Le développement des globules sanguins chez les Amniotes." *Bibliographie Anatom.* t. x.

[2] Maximow. "Die frühesten Entwickelungstadium der Blut und Bindegewebezellen beim Säugetierenembryo." *Archiv Mikr. Anat.* B. lxxiii.

[3] M. B. Schmidt. "Über Blutzellenbildung in Leber und Milz." *Ziegler's Beiträge,* B. ii, 1892.

[4] Lobenhoffer. "Über extravasculäre Erythropoëse in der Leber." *Ziegler's Beiträge,* B. xliii, 1908.

[5] Jost. "Beitrag zur Lehre von der Entwicklung des embryonales Rindes." *Archiv f. Mikr. Anat.* B. lxi, 1903.

[6] Schridde. "Die Entstehung der ersten embryonalen Blutzellen." *Verhandl. d. Deutsch. path. Gesellsch.* 1907.

Maximow lui-même est d'avis que les globules sanguins du foie embryonnaire proviendraient de jeunes cellules mésenchymateuses situées entre l'endothélium et les cellules hépatiques.

L'auteur fait remarquer que certaines cellules hépatiques pourraient être confondues avec de volumineux lymphocytes dont l'origine serait mésenchymateuse.

L'opinion de Maximow au sujet des cellules endothéliales des vaisseaux, c'est qu'elles peuvent, en se divisant, donner naissance à des cellules du sang en dehors des parois vasculaires elles-mêmes. Lambin[1] dans l'excellente revue qu'il a donnée de l'état actuel de l'hématologie morphologique, croit que les éléments sanguins du foie dérivent de l'hémohistioblaste de Ferrata, puisqu'ils proviennent de cellules mésenchymales polymorphes, et peut-être en partie de cellules endothéliales, ou d'éléments immigrés.

Enfin, J. Jolly et Th. Saragea[2], dans une séance de la Société de Biologie de Paris, en 1922, ont donné les résultats d'une étude sur les ébauches sanguines embryonnaires intrahépatiques.

Au 13me ou au 14me jour on voit apparaître dans les travées, des cellules lymphoïdes volumineuses semblables aux hématogonies de l'aire vasculaire.

Ces éléments ne se forment pas aux dépens des cellules hépatiques, qui en sont toujours distinctes, par l'aspect de leur noyau et de leur protoplasme. On ne voit pas non plus, d'après ces auteurs, les cellules endothéliales se transformer en cellules lymphoïdes, ni les cellules mésenchymateuses intrahépatiques d'ailleurs peu nombreuses, les constituer.

L'origine des grosses cellules lymphoïdes, qui seraient d'après eux la source des globules sanguins dans le foie, leur est inconnue. Peut-être proviennent-elles d'éléments conjonctifs du mésenchyme intrahépatique, mais ils n'ont pu le vérifier d'une manière absolument sûre. Ce que nous avons observé, font remarquer ces auteurs, est plutôt en faveur de l'opinion qui voit dans ces éléments lymphoïdes originels, des cellules intrasanguines qui se sont introduites entre les cellules hépatiques, etc.

Durant un séjour au laboratoire d'histologie de University College of London, Monsieur le Professeur J. P. Hill eût l'extrême obligeance de mettre à ma disposition une importante collection d'embryons de lapins, depuis 8 mm. et un peu moins de longueur, de 9 mm., 10 mm., 11½ mm., 14 mm., 28 mm., et 64 mm. Ce matériel devait servir, dans ma pensée, à une étude sur les neurofibrilles qui me parût momentanément impossible à exécuter. Je l'utilisais en vue de la solution d'un autre problème, celui de l'origine des cellules sanguines dans le foie embryonnaire.

Les embryons ont été fixés par les différents fixateurs employés couramment pour les études d'embryologie. Ils ont été colorés par l'hématoxyline de Delafield, de Ehrlich, l'éosine, l'orange, etc.

[1] "L'état actuel de l'hématologie morphologique." *Revue de Questions Scientifiques*, Janvier et Avril, 1923.
[2] Société de Biologie, 1922.

Les coupes ont été faites en séries complètes.

Tel est le matériel d'études qui a fait l'objet des observations relatées dans ce travail, qui n'est qu'une introduction à une étude plus étendue et comparée, dans laquelle nous insisterons d'avantage sur les structures cytologiques.

Toutes les observations ont été faites à l'objectif à l'immersion $\frac{1}{2}$ in. Watson, et à l'oculaire 12.

Les dessins ont été faits à la chambre claire de Leitz.

Notre intention est de démontrer:

1°. Que le foie commence par présenter une plasmodie, constituée par des noyaux disposés sans ordre dans une masse protoplasmique vacuolisée, et traversée par quelques capillaires.

2°. Dans cette plasmodie, on observe des noyaux en division mitotique, qui s'entourent d'une zone protoplasmique granuleuse éosinophile, qui se détache de la plasmodie et s'isole. L'ensemble forme une cellule sanguine semblable à celles, encore rares, qui se trouvent à l'intérieur des capillaires. Cette formation discrète de globules sanguins se continue ainsi jusqu'au 14me ou au 15me jour de la vie embryonnaire.

3°. A partir du 14me ou du 15me jour, la production des globules sanguins devient très grande. La division des noyaux des cellules hépatiques se fait d'abord par mitose. Les noyaux des cellules-filles provenant de cette division se divisent eux-mêmes rapidement par amitose, constituant des cellules plus petites à noyaux en état de pycnose, que l'on observe dans le tissu hépatique et à l'intérieur des capillaires. Dans ceux-ci, les nouvelles cellules sanguines perdent leur noyau. On observe toujours à cette période et plus tard quelques cellules sanguines anucléées.

A cet effet, nous donnons une description aussi brève que possible du tissu hépatique des embryons des différents stades que nous avons signalés plus haut. Nous nous excusons d'entrer dans des détails qui, à première vue, paraissent avoir peu d'utilité, mais qui sont en réalité très importants pour la démonstration que nous devons faire.

Nous lui adjoignons des dessins aussi exacts que possible, avec les explications utiles.

Embryon de lapin de 8 mm. de longueur.

Le foie de cet embryon présente un grand intérêt au point de vue de la formation des globules rouges.

Le tissu hépatique forme des travées encore peu nombreuses, séparées par des vaisseaux, de grands capillaires *v.v.*, fig. 1, qui sont bien délimités par des cellules endothéliales.

Les travées hépatiques peu volumineuses sont constituées par une plasmodie dans laquelle on observe de nombreux noyaux. La plupart de ceux-ci se reconnaissent facilement à leur forme, et surtout à leur structure; ce sont des noyaux hépatiques, *a*, fig. 1. On ne peut les confondre avec les cellules

endothéliales des vaisseaux qui bordent les travées et qui sont aplatis, *b*, fig. 1.

La plupart sont des noyaux au repos, au sein d'un protoplasme indivis.

Il en est qui sont en état de division, *c*, fig. 1. On en trouve à divers stades de division, prophase, début de prophase, ou fin de prophase, métaphase, etc.

Il est important de constater que le protoplasme se modifie autour de ces noyaux en division; il est plus granuleux et il se délimite nettement du restant de la plasmodie.

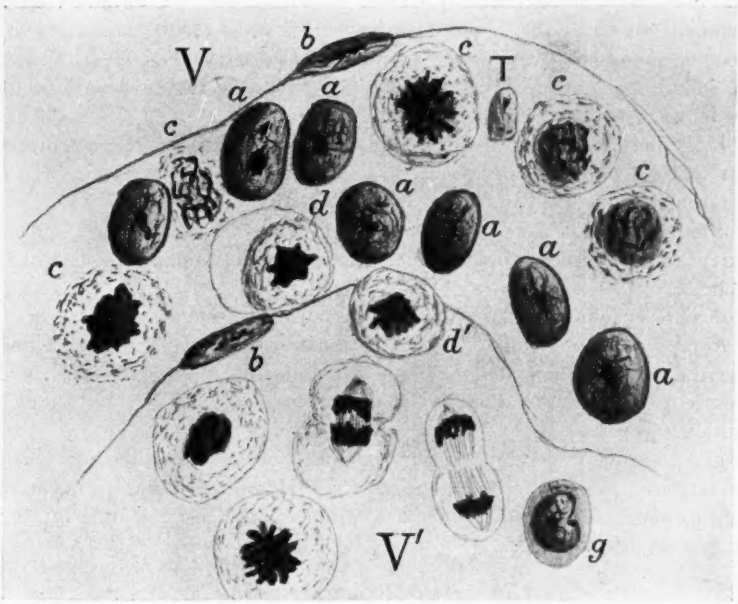

Fig. 1.

Il se forme ainsi une cellule libre, fig. 1, *d*, qui se trouve souvent au niveau d'une grande vacuole. Sur le bord du capillaire tout proche, on observe une cellule, *d'*, tout à fait semblable aux cellules intravasculaires qui semble se détacher de la plasmodie. Arrivée dans le capillaire, la cellule, qui est au début de la division, poursuit les différentes étapes de celle-ci. Aussi, peut-on observer, dans les vaisseaux capillaires, des globules rouges à tous les stades de la division, fig. 1, *V'*.

Nous n'en donnons dans le dessin que quelques exemples, mais en réalité ils sont très nombreux. Nous en ferons bientôt une étude cytologique en employant les méthodes de fixation et de coloration appropriées.

Nous avons observé également dans les capillaires des cellules présentant

un volumineux noyau au repos entouré d'une mince bande protoplasmique granuleuse.

Ce noyau resemble beaucoup au noyau de la cellule hépatique; mais il présente quelquefois un commencement de lobulation, fig. 1, *g*.

Ces cellules sont beaucoup moins nombreuses que les globules rouges; elles ont l'aspect, la structure de certains globules blancs.

En résumé, nous observons dans l'embryon de 8 mm. des noyaux hépatiques en division qui s'entourent d'une zone protoplasmique bien délimitée, éosinophile; l'ensemble constitue une cellule bien différenciée qui s'isole, se détache de la plasmodie, et qui finit par tomber dans la lumière d'un grand vaisseau, quand elle est située sur le bord de la travée; ou qui se trouve dans une grande vacuole, quand elle s'est formée au milieu de la plasmodie. La fig. 1 donne une idée imparfaite de la structure d'une partie de travée hépatique d'un très jeune embryon de lapin de 8 mm.

V, *V'* indiquent les vaisseaux volumineux bordant la travée; *a* représente les noyaux hépatiques au repos de la plasmodie.

b répresente un noyau de cellule endothéliale.

c représente des noyaux hépatiques à divers stades de division, qui s'entourent d'une zone protoplasmique, granuleuse, éosinophile, nettement différenciée.

d représente une cellule isolée, au niveau d'une grande vacuole.

d' représente une cellule isolée qui se détache de la plasmodie, et qui se trouve à peu près complètement dans la lumière d'un grand vaisseau, *V'*, dans lequel on trouve d'autres cellules semblables, dont le noyau est en division.

g représente des cellules, qui sont probablement des globules blancs. On retrouve presque toujours auprès des noyaux en division un noyau tout proche, plus petit, presqu'incolore, que nous considérons comme un noyau de tréphocytes, fig. 1, *T*.

Embryon de 10 *jours* (9 *mm.*).

Le bourgeon hépatique se présente à cet âge sous forme d'une masse protoplasmique parsemée de noyaux, légèrement granuleuse et filamenteuse, indivise, et présentant de nombreuses vacuoles, grandes et petites. Nous en avons indiqué quelques-unes dans la fig. 2, *v*.

Il est formé, en un mot, d'une vaste plasmodie constituée par un grand nombre de noyaux, séparés les uns des autres par un métaplasme vacuolisé.

De larges vaisseaux à parois très minces renferment des globules rouges nucléés, *cs*, fig. 2. Il n'y a pas de tissu mésoblastique, semble-t-il, qui ait pénétré dans le bourgeon à cette époque. Seul un épithélium aplati l'enveloppe. Les noyaux de la plasmodie se ressemblent, quant à la forme et à la structure. Leur forme est arrondie ou allongée; cette dernière est la plus fréquente.

Leur structure est réticulée, à trabécules courts, épais, peu nombreux, qui adhèrent à quelques petites masses nucléiniennes condensées, parmi lesquelles,

une plus volumineuse forme un nucléole. Dans les mailles, il y a une substance amorphe, souvent fortement teintée par l'hématoxyline. Il en est cependant d'un volume beaucoup plus petit peu colorés, *T*, *T*. Ils se trouvent d'ordinaire dans le voisinage immédiat de noyaux en division. Nous les considérons comme des tréphocytes. Cette observation corrobore celles que nous avons faites dans un récent travail[1].

Il en est d'autres encore qui présentent divers stades de division nucléaire.

La fig. 2 A présente à droite une plaque équatoriale et un fuseau. Chose importante à noter, c'est que ce noyau en division est entouré d'une masse

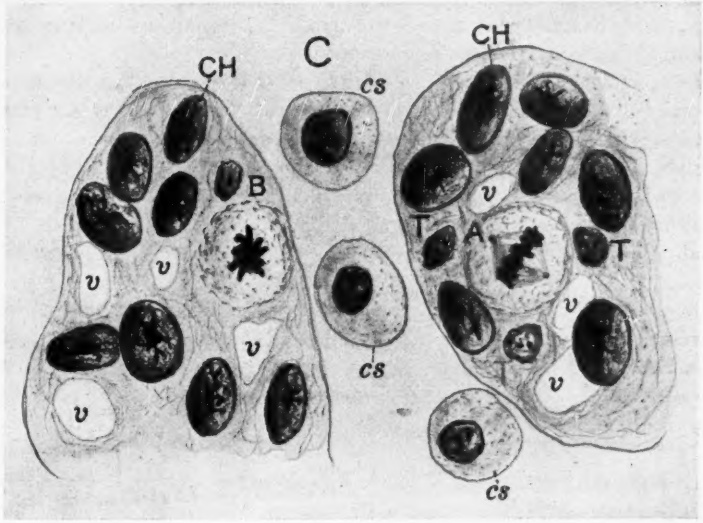

Fig. 2.

protoplasmique parfaitement limitée, alors que tous les autres noyaux voisins sont dans une masse protoplasmique indivise.

Notons encore que le protoplasme entourant le noyau en division est granuleux; les granules se colorent par l'éosine d'une manière assez intense. Il y a aussi dans le protoplasme des filaments.

La figure 2 B représente à gauche un noyau en division, dont le stade est plus difficile à déterminer mais qui est entouré par une masse protoplasmique parfaitement délimitée du restant de la plasmodie. La structure du protoplasme est ici aussi la même; granules colorés par l'éosine, filaments; l'ensemble donne au protoplasme une teinte rosée.

Il semble donc qu'autour de ces noyaux en division, le métaplasme se soit

[1] *Les cellules accompagnatrices ou tréphocytes chez les animaux.* Société scientifique de Bruxelles, 1925.

découpé et différencié, de manière à former des cellules isolées dans la plasmodie. Ces cellules sont généralement arrondies, volumineuses, aussi volumineuses que la plupart des cellules sanguines *cs* qu'on observe dans le grand vaisseau *C*; leur structure protoplasmique est identique à celle des globules sanguins qui se trouvent dans les vaisseaux.

Notons de plus que ces cellules apparaissent au sein de la plasmodie hépatique, dans le voisinage de grandes vacuoles.

Ces différentes constatations montrent qu'il s'agit ici, d'un mode de formation de globules rouges dans le foie de l'embryon du lapin, aux dépens de la plasmodie hépatique.

La division du noyau partage les chromosomes en deux masses assez égales. Le protoplasme se divise également, la division donne deux cellules qui souvent se trouvent dans une grande vacuole.

Quelquefois, la division du protoplasme ne se fait pas, et l'on observe dans ce dernier deux masses nucléaires. Il n'est pas rare d'observer des globules sanguins, dans les grands vaisseaux, possédant deux masses nucléaires semblables.

Il est intéressant de noter que les vacuoles les plus volumineuses sont parfaitement limitées par un noyau qui ressemble tout-à-fait à un noyau hépatique, légèrement aplati et un peu recourbé du côté de la cavité des vacuoles.

On peut supposer que ce noyau est un noyau hépatique qui est destiné à devenir un noyau de cellule endothéliale, qui borde un capillaire en voie de formation. Il n'est pas impossible que certains capillaires puissent se former de la sorte, et commencer par une large vacuole creusée dans le protoplasme de la plasmodie.

Il y a des noyaux en division qui ne s'entourent pas d'une zone protoplasmique, à granules éosinophiles, et qui ne s'isolent pas; ils restent des noyaux hépatiques; tandis que ceux que nous venons d'étudier, s'entourent dès les premiers stades de division, d'une zone protoplasmique bien délimitée, éosinophile; ils constituent par là des éléments spéciaux, distincts, qui se détachent de la plasmodie, et qui deviennent des globules sanguins de l'embryon. Ils ont les mêmes caractères morphologiques, la même structure que les cellules sanguines intravasculaires. Il est important d'observer les bords des travées hépatiques parce que l'on voit plus facilement à ce niveau, que les nouvelles cellules sanguines se forment de la plasmodie hépatique, et qu'elles peuvent s'en détacher pour tomber dans la lumière des vaisseaux.

Si l'on observe, en effet, la plasmodie hépatique dans la partie qui borde les grands vaisseaux, on remarque souvent des cellules qui sont sur le point de s'en détacher et qui font hernie dans la lumière du vaisseau. On observe de plus, que ces cellules ont la même forme et la même structure que beaucoup de cellules sanguines intravasculaires. La fig. 3, *d*, en donne un exemple. Il ne peut être question ici, ni d'une cellule endothéliale, ni d'une cellule mésenchymateuse, qui se différencierait et formerait une cellule sanguine. Il s'agit

bien ici d'éléments hépatiques qui se divisent pour former des cellules sanguines nouvelles, dont l'une est sur le point de se libérer et de tomber dans la lumière d'un vaisseau.

La figure 3 représente une minime partie d'une travée hépatique d'un embryon de lapin de 10 jours.

a représente les noyaux hépatiques formant, avec le métaplasme, la plasmodie hépatique.

b représente des noyaux hépatiques au début de la division, en prophase.

c, noyau hépatique en division, probablement à la métaphase.

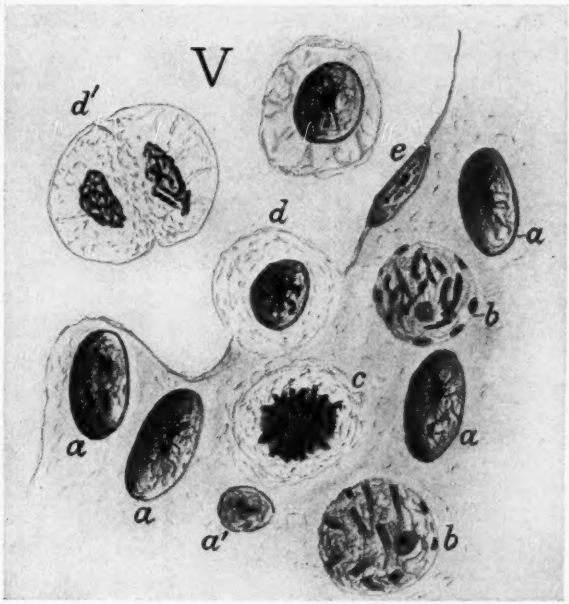

Fig. 3.

d, cellule prête à se détacher de la travée, et à tomber dans le vaisseau *V*, dans lequel on observe des cellules semblables quant à leur forme, leur structure, leur volume. On observe une cellule sanguine en division, au stade de la télophase. Le protoplasme de ces cellules contient des granules très fins qui se colorent un peu plus intensément par l'éosine. L'ensemble du protoplasme est coloré en rouge vif.

Le protoplasme entourant le noyau *c* en division est parfaitement délimité du restant de la plasmodie. Il contient un grand nombre de granules éosinophiles. Noyau et protoplasme rappellent ceux des cellules sanguines. Un petit noyau *a'*, peu riche en nucléine, et déformé, se trouve dans le voisinage immédiat de la cellule en division. C'est, probablement, un élément tréphocytaire.

La remarque importante à faire comme conclusion des observations que nous avons recueillies jusqu'ici au sujet des travées hépatiques à peine ébauchées de l'embryon de 10 jours, c'est que des éléments nettement délimités se forment et se détachent de la plasmodie; que ces éléments différenciés ont la même forme, le même volume, la même structure que les cellules sanguines situées dans les vaisseaux, et enfin que l'on observe souvent ces éléments à moitié détachés de la travée, sur les bords de celle-ci, prêts à tomber dans le vaisseau ou au sein de grandes vacuoles au milieu de la travée. La figure 4 peut constituer une nouvelle preuve de la formation de cellules sanguines aux

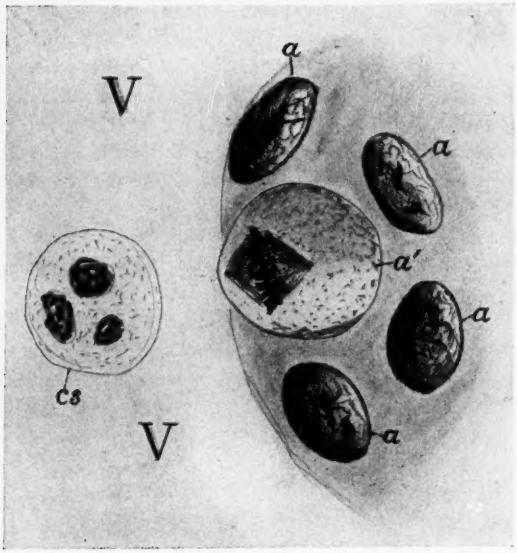

Fig. 4.

dépens des éléments hépatiques des travées. *V* représente la lumière du vaisseau dans lequel on observe *cs*, cellule sanguine à noyau un peu irrégulier, provenant probablement de ce que à la télophase les chromosomes se sont disposés en plusieurs amas.

a, noyaux hépatiques au sein du métaplasme.

a', noyau en division, métaphase, entouré de protoplasme parfaitement délimité, constituant un élément, une cellule nettement distincte. Elle fait hernie dans la lumière du vaisseau, dont rien ne la sépare. A la télophase, la cellule-fille la plus rapprochée de la lumière tombera nécessairement dans le vaisseau *V*. La division se fait, comme on le voit dans une partie de la cellule qui est très proche de la lumière du vaisseau.

Il semble que ces jeunes embryons que nous venons d'étudier, sont d'une

grande importance au sujet de l'origine hépatique, hypoblastique, des globules du sang dans le foie de l'embryon. Le phénomène est plus facile à observer, parce que les cellules sont plus grandes et moins nombreuses ici que dans les embryons plus âgés que nous allons étudier.

Embryons de 11 *jours.*

Le bourgeon hépatique ressemble beaucoup à celui de l'embryon de 10 jours. Il représente une vaste plasmoïde découpée par des vaisseaux volumineux. Le protoplasme contient une grande quantité de noyaux de même

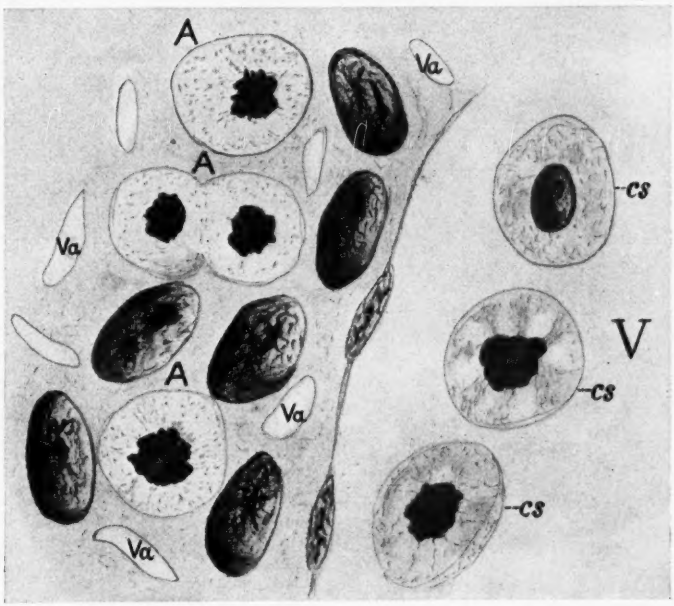

Fig. 5.

structure, et de très nombreuses vacuoles, *Va*, fig. 5. Autour de certains noyaux, le protoplasme est parfaitement délimité; noyaux et protoplasme forment à ces endroits là seulement, des cellules nettement différenciées, et isolées de la masse plasmodiale hépatique. Ces cellules ont la même forme, le même volume, la même structure, le même aspect que les cellules sanguines, situées dans les grands vaisseaux.

La figure 5 représente une petite partie de la plasmodie constituant le jeune bourgeon hépatique. Les noyaux possèdent tous la même structure réticulée, grossière, à trabécules souvent épaisses courtes, peu nombreuses.

Le métaplasme est granuleux, filamenteux, peu abondant, et possède de nombreuses vacuoles, *Va*.

A, *A*, *A* représentent les cellules découpées, isolées dans la plasmodie. Ces cellules ont la même forme, le même aspect, la même structure que les cellules sanguines *cs* des grands vaisseaux *V*.

La figure 6 représente une partie de la plasmodie longeant le vaisseau *V*. Le bord de celle-ci présente en *A* une cellule qui s'en détache et qui est semblable aux cellules sanguines, intravasculaires.

Avant de poursuivre l'examen du foie d'embryons plus âgés, récapitulons nos observations.

Dans les bourgeons hépatiques de très jeunes embryons de 10 et de 11

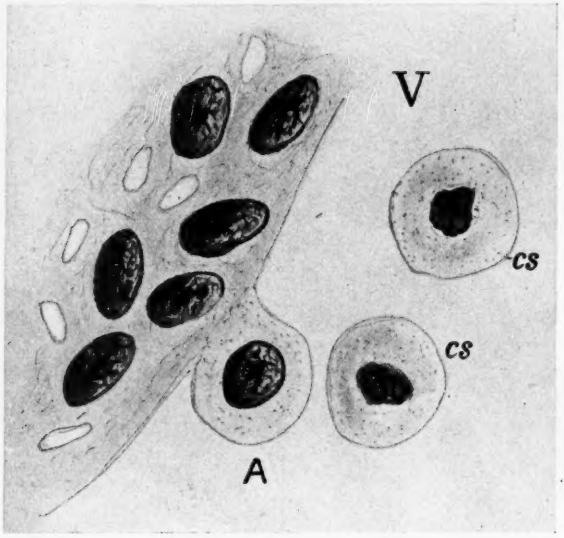

Fig. 6.

jours, on observe une masse protoplasmique multinucléée, une plasmodie contenant deux sortes de noyaux: (1°) les noyaux hépatiques proprement dits sont les plus nombreux; le protoplasme qui les entoure présente de nombreuses vacuoles.

(2°) Il en est de plus intensément colorés, présentant l'une ou l'autre phase de la division nucléaire. Ils sont entourés d'une zone protoplasmique nettement délimitée, finement granuleuse, colorée par l'éosine. Ce sont les seuls éléments nettement circonscrits du bourgeon hépatique.

Ils se détachent de ce bourgeon et entrent dans le courant sanguin. Ces nouvelles cellules sanguines ou hématogonies apparaissent dans le bourgeon hépatique, au moment où on n'observe guère que des éléments hépatiques. On peut se convaincre facilement, en observant les préparations, que de

nombreuses cellules sanguines nouvelles proviennent des bords des travées hépatiques. La figure 3, *d*, et la figure 6, *A*, reproduisent deux exemples de cette formation de cellules sanguines nouvelles aux dépens des bords des travées hépatiques. Dans toutes les préparations de travées hépatiques de très jeunes embryons, on peut recueillir des exemples semblables, qui prouvent l'origine hépatique, par conséquent hypoblastique, de cellules sanguines dans le foie embryonnaire.

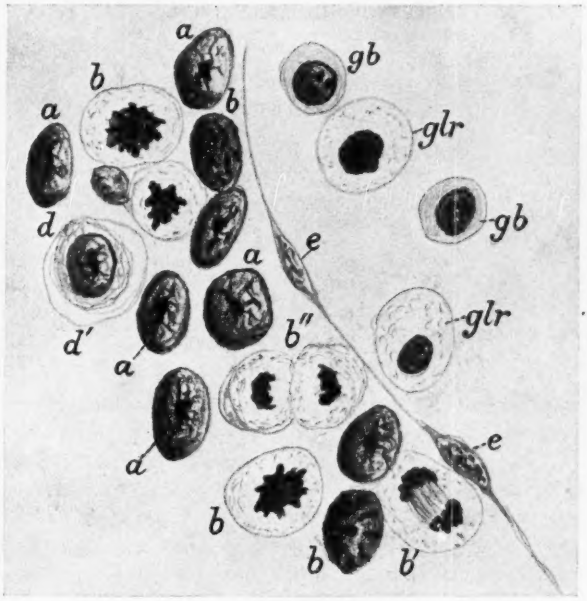

Fig. 7.

Embryon de 13 *jours.*

On observe dans le foie de cet embryon des travées hépatiques bien développées, entre lesquelles on distingue de grands vaisseaux. Au sein des travées il y a des capillaires très reconnaissables à leur forme et à leur structure. Il y a beaucoup de noyaux à l'état de repos. Quelques-uns présentent des figures de division. Figure 7, *b*, *b'*, représente divers stades de division, prophase, métaphase, télophase.

En *b''* on observe la division d'une cellule provenant de la plasmodie hépatique qui forme deux cellules semblables à celles que l'on trouve dans le grand vaisseau *V*, *glr*.

gb représente des globules blancs.

En *d* on voit un noyau entouré d'une zone protoplasmique qui se détache du syncitium au niveau d'une grande vacuole. Le noyau de cette nouvelle cellule n'a guère changé de forme ni de structure; il est un peu plus petit peut-être que les noyaux voisins. D'un autre côté, il est entouré d'une très mince couche de protoplasme. Il est probable qu'il s'agit de la formation d'un globule blanc, par transformation d'un élément hépatique.

Il semble qu'à cette période du développement les divisions cellulaires deviennent plus nombreuses. Il est très rare de voir des cellules endothéliales en division. *e*, fig. 7, cellules endothéliales.

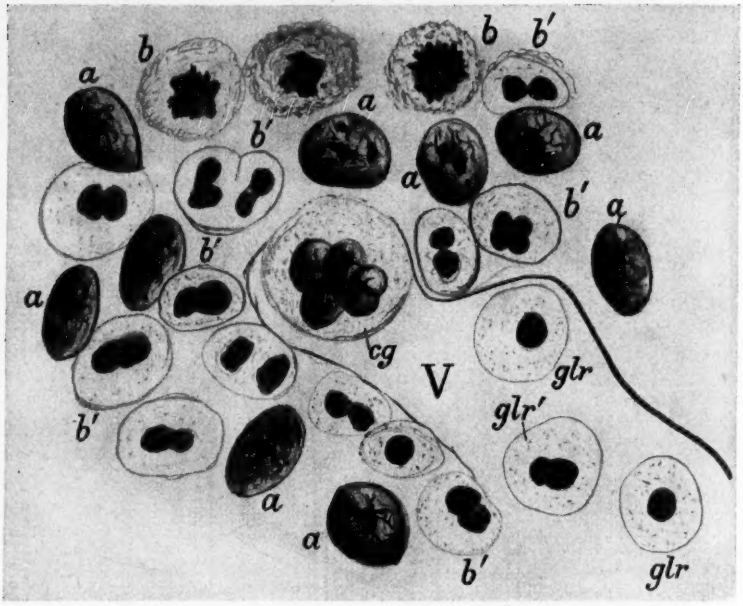

Fig. 8.

Embryon de lapin d'environ 14 *jours*, 10 *mm., coloration cochenille orange G.*

Les travées hépatiques présentent à peu près les mêmes structures. La formation des cellules sanguines est à cette période plus intense que dans la foie de l'embryon précédent.

Les noyaux hépatiques au repos apparaissent de même forme, de même structure et à peu près de même grandeur que ceux de l'embryon de 13 jours.

Un vaisseau *V*, fig. 8, présente une quantité de globules rouges, dont le protoplasme est coloré en jaune par l'orange G. Les noyaux sont colorés en rouge. Au bord du vaisseau, on observe une masse protoplasmique volu-

mineuse contenant cinq ou six noyaux, qui se fusionnent. Cette masse protoplasmique nucléée est prête à se détacher et à être emportée par le courant sanguin. Elle va former une cellule géante, *cg*.

Les autres noyaux hépatiques présentent divers stades de division, comme nous l'avons vu précédemment.

Mais il y a ici des divisions successives et rapides des noyaux; on voit en effet au niveau du bord de la travée, dans le voisinage immédiat du vaisseau, *V*, une grande quantité de cellules sanguines dont les noyaux sont en division.

La seconde division se fait, à n'en pas douter, par division directe, fig. 8, *b'*.

On voit en effet sur le bord de la travée des masses nucléaires présentant des étranglements, *b'*, qui donnent aux noyaux l'aspect de deux masses chromatiques à peu près égales, intensément colorées par l'hématoxyline ou les colorants nucléaires. Le protoplasme se divise souvent en même temps. Il peut se faire que la division du protoplasme ne se produise pas, *b'*. Il existe en ce cas deux masses nucléaires plus ou moins nettement séparées dans une seule cellule. Il y a d'abord une division mitotique, dont les télophases ne sont pas suivies de la formation de nouveaux noyaux présentant une structure réticulée ordinaire.

Les chromosomes de la télophase forment deux masses qui au lieu de constituer deux nouveaux noyaux ordinaires, se scindent chacune en deux portions qui vont constituer, par division directe, deux noyaux plus petits. La division des noyaux s'accompagne de la division du protoplasme, de manière à constituer de nouvelles cellules sanguines, qui présentent nécessairement un autre aspect que les cellules sanguines des embryons plus jeunes. Les noyaux sont constitués par une masse nucléinienne assez compacte comme s'ils étaient en pycnose, et nous pensons que c'est bien l'état de pycnose du noyau qui les caractérise. La séparation des deux masses nucléaires peut se faire soit dans la travée même, soit dans la lumière des vaisseaux.

Ces masses nucléaires sont destinées à disparaître comme nous l'observons dans des embryons plus âgés.

Par contre le protoplasme se colore de plus en plus intensément par l'éosine.

Embryon de 15 *à* 16 *jours*, 11½ *mm.*

Le foie de cet embryon présente à peu près les mêmes structures, et nous permet de voir comment les globules rouges du sang de l'embryon peuvent naître du bourgeon hépatique. Les noyaux hépatiques ont leur structure ordinaire. Ils se trouvent au sein d'une masse protoplasmique encore indivise mais dont certaines parties cependant commencent à se découper. Il y a des noyaux entourés d'une zone protoplasmique sombre; d'autres sont entourés d'un protoplasme plus clair, mais légèrement granuleux et colorable par l'éosine.

En ce dernier cas, les noyaux sont souvent en état de division.

Il y a donc ici des cellules sombres et des cellules claires. Cet aspect dépend en partie de la fixation et de la coloration et aussi de la composition

du protoplasme qui entoure les noyaux. Il apparaît mieux quand, par exemple, la décoloration de l'hématoxyline n'a pas été poussée trop loin, et dans ce cas les préparations sont moins claires, et plus difficiles à analyser.

On trouve aussi dans la figure 9 des noyaux de cellules hépatiques, à divers stades de division, jusqu'à la formation de nouveaux globules rouges, dont le noyau et le protoplasme ont la même structure que ceux des globules rouges qui se trouvent dans les vaisseaux. En *b'* on observe des divisions directes. Les cellules endothéliales ont un noyau qui est toujours ou presque toujours au repos. Il est rare de constater des figures de division dans ces

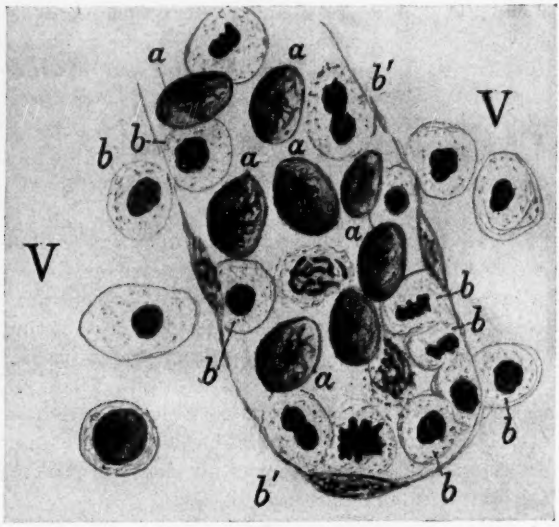

Fig. 9.

cellules. Plusieurs observateurs voudraient cependant en faire une source importante de globules rouges.

Le foie de ces embryons de lapin possède des parties très différentes les unes des autres au point de vue de la formation des globules rouges. Il y a des points qui présentent une véritable fonte du tissu hépatique, et qui se transforment en amas de cellules sanguines. On voit en ce cas une quantité considérable de globules rouges à tous les stades de leur formation, de globules blancs, et de cellules hépatiques séparées les unes des autres, ou réunies en de petits amas de trois ou de quatre éléments. Parmi elles on trouve, de temps en temps, une masse protoplasmique colorée par l'éosine et contenant quelques noyaux hépatiques qui commencent à se réunir et à se fusionner. L'ensemble va former une cellule géante.

A ces endroits de fonte la structure ordinaire des travées a disparu.

Embryon de lapin de 14 *mm.* (18 *jours environ*).

On observe dans ce foie la formation de travées régulières, rayonnantes, séparées les unes des autres par de très petits capillaires qui aboutissent à un vaisseau plus volumineux.

Les travées sont formées de noyaux hépatiques autour desquels on observe généralement une zone protoplasmique assez distincte. Ces noyaux ont une structure semblable à celles des noyaux que nous avons étudiés chez les embryons plus jeunes, fig. 10, *a*.

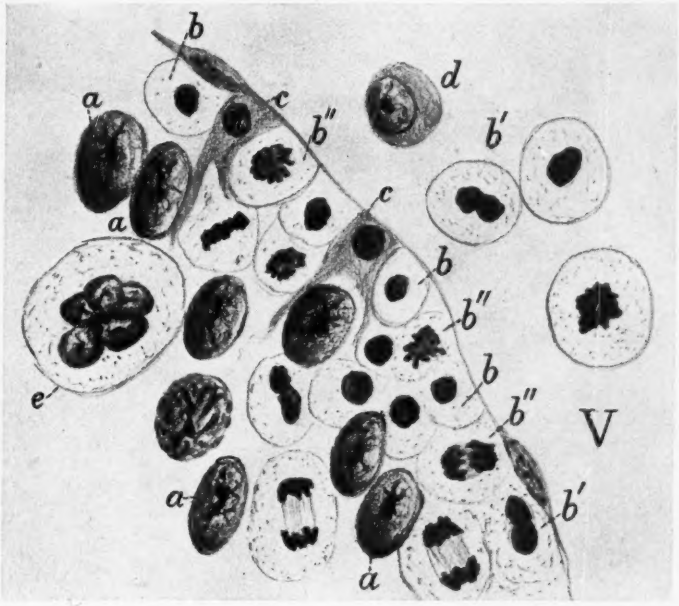

Fig. 10.

Le bord des travées, comme dans les foies déjà étudiés, présente un grand nombre de cellules en division, qui vont former des globules rouges semblables à ceux qui se trouvent déjà dans le vaisseau; *b*, *b'*, figure 10. Les cellules endothéliales sont reconnaissables à leur situation, leur volume, leur structure.

En dedans de ces cellules endothéliales on peut observer des cellules un peu spéciales, ayant un noyau arrondi à structure réticulée et granuleuse, à membrane épaisse, intensément colorée par l'hématoxyline.

Le protoplasme de ces cellules, souvent très dense et filamenteux, présente des prolongements dirigés entre les cellules hépatiques voisines et le long de

la paroi du vaisseau, *c*, *c*, fig. 10. Ce sont très probablement de jeunes cellules de Kupffer.

En *d* nous voyons un globule blanc du sang, dont le noyau a une structure qui ressemble beaucoup à celle des noyaux hépatiques. Le protoplasme qui l'entoure, et qui lui forme une couche épaisse d'un côté, prend les colorants basiques, alors que le protoplasme des globules rouges voisins se colorent par les colorants acides.

En *e*, fig. 10, nous reproduisons une cellule géante formée d'un protoplasme coloré par les colorants acides. On y voit réunis quelques noyaux dont la structure est semblable à celle des noyaux hépatiques. Parmi les globules rouges situés dans les vaisseaux, il en est de nombreux dont le noyau présente des signes de division. On constate quelquefois que les travées hépatiques disparaissent en certains points. Sous la poussée des globules rouges qui se sont formés sur place, dans les travées, il semble que les cellules hépatiques qui restent, sont dissociées. Celles-ci ressemblent aux cellules à noyau volumineux que nous avons observées déjà dans le sang des capillaires hépatiques d'embryons plus jeunes, et que nous avons regardées comme des globules blancs, probablement de grands lymphocytes, qui auraient une origine hépatique.

Parmi les futures cellules du sang, on en observe dont les noyaux se divisent par mitose *b''*, ou par amitose *b'*; *b* est le résultat de ces divisions, c'est-à-dire une cellule dont le noyau en état de pycnose forme une masse nucléaire sans structure bien nette, qui est intensément colorée par les colorants nucléaires, mais dont le protoplasme légèrement granuleux est fortement coloré par l'éosine.

Embryon plus âgé, de 28 mm. de longueur.

A cette période du développement embryonnaire, les cordons cellulaires hépatiques sont parfaitement délimités, et séparés les uns des autres, par des capillaires, qui contiennent une grande quantité de globules rouges nucléés, ou sans noyau.

Le noyau des globules rouges qui se trouvent, à cette période, dans les capillaires, est d'ordinaire petit, arrondi, très régulier. La masse chromatique est fortement colorée par l'hématoxyline. Il est souvent difficile d'en voir nettement la structure; on y distingue quelques gros granules. Le protoplasme est intensément coloré par l'éosine, sa structure est finement granuleuse. Il est parfois incolore, mais ses limites sont nettes. Très souvent, à la place du noyau, on observe une zone peu colorée par l'hématoxyline, en gris-clair; en ce cas, il semble que le protoplasme est coloré plus intensément par l'éosine.

A ce stade de l'évolution embryonnaire, le foie paraît former une quantité considérable de globules rouges du sang. Ceux-ci ne proviennent pas des cellules endothéliales des capillaires, qui n'apparaissent que très rarement en état de division.

Ils proviennent des cellules du foie. En effet, dans la coupe d'une travée hépatique on observe:

(1°) Les noyaux caractéristiques du foie, autour desquels le protoplasme semble être plus ou moins bien circonscrit.

(2°) A côté de ces noyaux au repos il existe d'autres noyaux en division, qui présentent des phases différentes de la division des noyaux hépatiques.

Le noyau hépatique qui, au repos, a un aspect caractéristique change, en ce cas, d'aspect et de structure, suivant que la division est au stade de prophase, de métaphase, d'anaphase ou de télophase.

C'est ici, nous semble-t-il, que réside le point important de la question de l'origine des globules sanguins dans le foie embryonnaire. Il s'agit de montrer que la division de certains noyaux hépatiques donne naissance à des cellules, qui ressemblent en tous points aux globules sanguins intravasculaires.

Or, nous trouvons tous les stades de division du protoplasme et des noyaux hépatiques, depuis la prophase, jusqu'à la télophase, pour aboutir à la formation de cellules semblables aux cellules sanguines. C'est surtout sur les bords des cordons hépatiques, dans le voisinage immédiat des vaisseaux, qu'on observe ces stades de division, surtout des télophases.

Il est important de remarquer que ces noyaux en division sont entourés d'une zone de protoplasme bien délimitée et colorée intensément par l'éosine.

La structure de ces noyaux est un peu différente suivant l'étape où en est arrivée la télophase. Tantôt les chromosomes sont encore visibles, tantôt les chromosomes se sont tellement rapprochés qu'ils ne forment plus qu'une masse très dense, parfois uniformément et intensément colorée. Il est rare que les nouveaux noyaux issus de la télophase présentent un réseau chromatique bien reconstitué. Avant même que cette reconstruction du réseau nucléaire n'apparaisse, les noyaux nouveaux peuvent présenter de nouvelles divisions, non plus mitotiques, mais directes.

Durant toutes ces transformations nucléaires, une zone protoplasmique périnucléaire se colore par l'éosine ou par l'orange G.

Telle est l'origine des cellules souvent nombreuses que l'on observe sur les bords des travées hépatiques; elles sont prêtes à passer à l'intérieur des vaisseaux, et on en voit un certain nombre, faisant hernie dans la lumière de ceux-ci, à peu près détachées du tissu hépatique qui leur a donné naissance.

L'endothélium vasculaire forme une membrane très mince, qui n'est qu'une barrière très facile à franchir; les nouvelles cellules sanguines peuvent écarter, refouler les cellules endothéliales au voisinage desquelles elles s'accumulent, et elles peuvent faire facilement irruption dans les vaisseaux.

En divers endroits l'endothélium peut faire défaut, d'après certains auteurs; les nouvelles cellules sanguines sont en ce cas facilement entraînées dans les vaisseaux, où elles deviennent libres.

Les cellules sanguines intravasculaires et les cellules extravasculaires, séparés par l'endothélium vasculaire, ont la même forme, le même aspect, la même structure.

Elles ne constituent qu'une seule espèce de cellules qui proviennent, comme nous venons de le montrer de la division, par mitose et par amitose de certaines cellules hépatiques.

Tel est, dans ses grandes lignes, le processus de formation des cellules sanguines dans le foie embryonnaire du lapin.

Il faut noter que toutes les cellules hépatiques ne nous paraissent pas aptes à produire de nouvelles cellules sanguines. Celles-ci proviennent de cellules hépatiques en division, qui présentent autour du noyau une zone protoplasmique éosinophile, ou fortement colorée par l'orange G.

Si ce processus est vrai, il s'en suit que dans le foie embryonnaire, les nouvelles cellules sanguines ne proviennent pas exclusivement comme certains auteurs le prétendent, ni de cellules mésenchymateuses, qui à cette époque sont très peu nombreuses; ni des cellules endothéliales, qui, pour la plupart, se présentent à l'état de repos; ni de la transformation, de changements protoplasmiques survenus dans les cellules hépatiques, qui deviendraient par là des cellules sanguines, comme le pense Aron; ni de cellules intrasanguines qui se seraient insinuées entre les cellules hépatiques, comme le prétendent Jolly et Saragea.

Observons une coupe d'une travée hépatique d'un embryon de 28 mm. de longueur, colorée par l'hématoxyline Delafield et l'éosine. Nous voyons figs. 11, 12, 13 et 14:

(1°) Des capillaires bien délimités. De grands vaisseaux contiennent un certain nombre de globules rouges, à noyau petit, formant une masse compacte de nucléine, entourée d'une zone protoplasmique bien délimitée, colorée en rouge par l'éosine. D'autres globules rouges ne présentent pas de noyau, ou du moins le noyau apparaît à peine teinté en gris-pâle, sans structure aucune. On en trouve aussi dans les vaisseaux capillaires.

(2°) Des noyaux hépatiques, dont la forme et la structure sont bien connues. Ce sont des noyaux au repos.

(3°) Des noyaux hépatiques en division, aux différents stades de prophase, métaphase, anaphase, télophase.

Au bord des travées hépatiques nous observons de nouvelles cellules sanguines, semblables à celles qui se trouvent à l'intérieur des vaisseaux. A ce niveau des divisions cellulaires successives et rapides ont lieu, sans que les noyaux, arrivés à la télophase, aient eu le temps de se reconstituer en réseaux. On observe souvent dans un seul champ microscopique, à peu près toutes les étapes de la formation de globules sanguins. A la prophase, le noyau hépatique présente des chromosomes plus ou moins distincts qui deviennent plus courts, plus épais, et plus intensément colorés, ainsi que le liquide nucléaire, à une étape plus avancée. Malgré ces différences de structure, le noyau hépatique conserve dans son ensemble la même forme et le même volume.

La figure 11 représente une partie de travée hépatique.

Le vaisseau *V* contient beaucoup de globules rouges nucléés et non-nucléés.

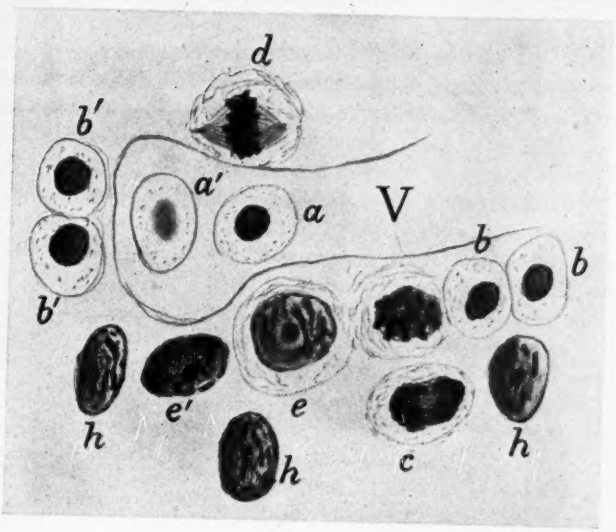

Fig. 11.

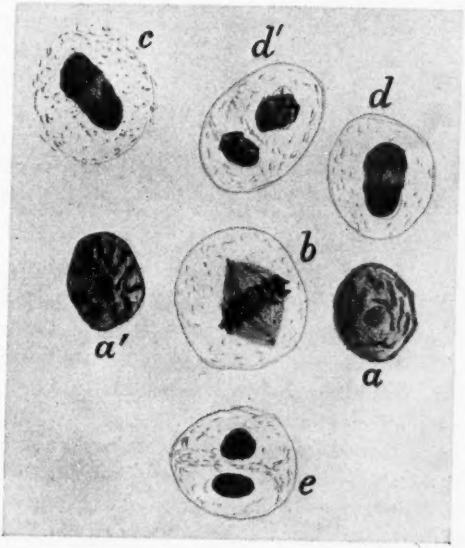

Fig. 12.

dont nous avons reproduit deux exemplaires *a* et *a'*. En dehors du vaisseau, les cellules *b*, *b* ressemblent en tout aux cellules *a*, *a'*.

Les cellules *b*, *b* sont le produit de télophases comme *c*. Ces télophases ont été précédées par des métaphases comme *d*. Celles-ci ont été précédées par des prophases comme celles qui sont représentées en *e*, *e'*. Le début d'une prophase est figuré en *e*. Les noyaux au repos sont figurés en *h*. Ce sont des noyaux hépatiques.

La figure 12 donne quelques autres exemples de division du noyau de la cellule hépatique:

a, *a'* noyau hépatique au début de la division à la prophase;

b, noyau hépatique à la métaphase;

c, *d*, noyau hépatique au stade de l'anaphase;

d', noyau hépatique au stade de la télophase;

e, formation de deux nouvelles cellules, complètement semblables aux cellules sanguines qui se trouvent dans les vaisseaux.

L'éosine colore une zone protoplasmique qui entoure le noyau. A la prophase cette coloration est très légère. Elle s'accentue à la métaphase et devient plus prononcée à la télophase. Lors de la formation des deux nouveaux noyaux, le protoplasme des deux nouvelles cellules est coloré par l'éosine, à peu près aussi intensément que le protoplasme des cellules sanguines intravasculaires. Il y a une gradation dans la coloration du protoplasme des nouvelles cellules sanguines, par l'éosine ou par l'orange G.

Nous admettons, avec MM. Jolly et Saragea, que les nouvelles cellules sanguines ne proviennent ni des cellules endothéliales, ni de cellules mésenchymateuses des travées hépatiques, ni de la transformation de la cellule hépatique en cellule sanguine, à la manière d'Aron. Nous doutons cependant qu'elles proviendraient de grosses cellules lymphoïdes, dont l'origine serait inconnue.

Nous pensons plutôt que les grosses cellules lymphoïdes de M. Jolly sont celles qui sont représentées en *b*, fig. 11 et en *e*, fig. 12, et qui proviennent, comme nous l'avons montré, de la division d'éléments hépatiques, de cellules du foie.

Embryon plus âgé, de 64 mm.

On a mesuré la longueur de la face dorsale de l'embryon, depuis le nez jusqu'à la partie caudale. En coupe transversale il paraît avoir une largeur à peu près double de celle de l'embryon de 28 mm.

Le foie présente en de nombreux points une véritable fonte du tissu hépatique, qui se change en globules sanguins.

Dans les autres parties du foie les noyaux ont leur forme et leur structure ordinaires. Il en est à l'état de repos. Leur membrane est intensément colorée, nettement délimitée, assez épaisse, uniforme, ou présentant des points épaissis. Ils possèdent généralement un volumineux nucléole, d'où partent des filaments peu nombreux, épais, qui se dirigent vers la membrane. Ce

nucléole est tantôt au centre du noyau, tantôt plus ou moins rapproché d'une de ses extrémités.

Quelques petits amas nucléaires, irréguliers, moins volumineux d'ordinaire que le nucléole, sont disséminés dans le noyau. Tous ces corps chromatiques sont intensément colorés par l'hématoxyline. Le liquide nucléaire l'est d'ordinaire beaucoup moins.

Parmi ces noyaux, beaucoup sont en division. On y observe les divers stades de division, semblables à ceux que nous avons décrits chez l'embryon de lapin de 28 mm.

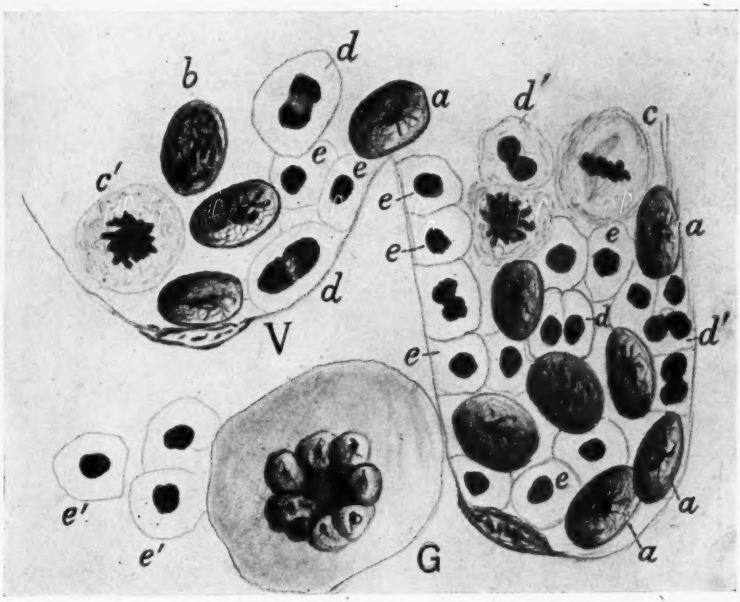

Fig. 13.

La figure 13 reproduit une coupe du foie de l'embryon de 64 mm.

a représente les noyaux hépatiques à l'état de repos.

b, *b* représente les premiers stades de la prophase.

c représente des métaphases.

c' représente des métaphases ou des anaphases vues en coupes transversales.

d représente des télophases. On y observe souvent deux masses compactes, qui se séparent et qui donnent deux cellules distinctes.

e, semblables aux cellules *e'*, qui se trouvent dans le vaisseau *V*.

Une seconde division intervient rapidement après la première; qui se fait par division directe, fig. 13, *d'*. Dans le vaisseau *V* on observe une cellule

géante *G*, présentant un noyau volumineux, qui provient de la fusion de plusieurs noyaux hépatiques. Le protoplasme entourant ce noyau lobé est une partie du protoplasme du syncitium qui forme le bourgeon hépatique.

La figure 14 représente une coupe de vaisseau *V*; les parois de ce dernier sont constituées par des cellules de forme et de structure diverses:

a, noyau hépatique au repos.

a', *a'*, noyaux hépatiques en état de prophase.

b, *b'*, noyaux hépatiques en division, au stade de la métaphase.

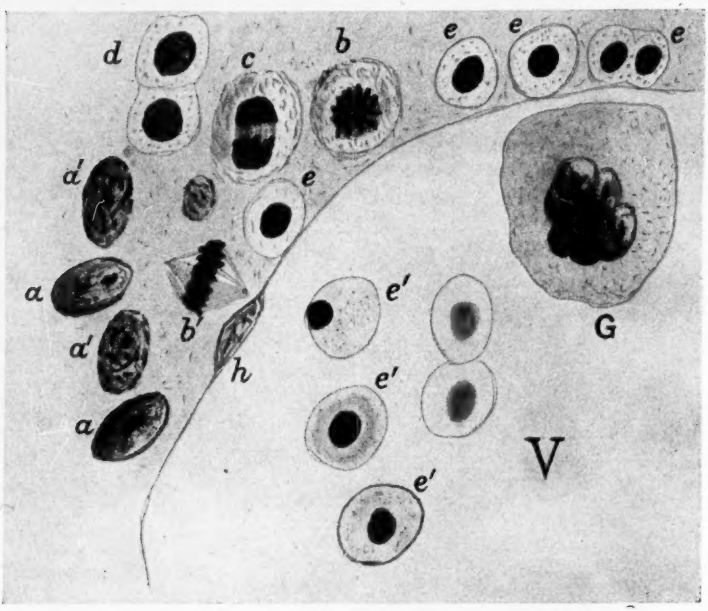

Fig. 14.

c, noyau hépatique en division, au stade de la télophase, l'anaphase étant à peine terminée.

Le noyau hépatique étant divisé en deux masses nucléaires, la télophase étant terminée, le protoplasme ne semble pas toujours participer à la division.

d, la division du noyau et du protoplasme est terminée; deux nouvelles cellules sont formées.

e, cellules sanguines nouvelles isolées, semblables à celles qui se trouvent en *e'*, *e'* dans le vaisseau.

A partir de la métaphase et même avant, dès la prophase, ces noyaux sont entourés d'une zone protoplasmique éosinophile. Cette coloration du protoplasme s'accentue à mesure que la cellule sanguine se différencie.

Il y a des noyaux en division, entourés d'un protoplasme qui reste incolore ou très peu coloré sous l'action de l'éosine. Ce sont des noyaux hépatiques, qui donnent de nouveaux éléments hépatiques. Il y a des globules rouges sans noyau ou à noyau à peine coloré. Il en est dont le noyau est situé à la périphérie de la cellule. En *G* on observe une cellule géante à noyau lobé, formé par la fusion de plusieurs noyaux hépatiques.

SOMMAIRE

L'étude du foie d'embryons de lapin, arrivés à divers stades d'évolution, nous permet de tirer les principales conclusions suivantes:

(1°) Le foie est une plasmodie, constituée par une masse protoplasmique vacuolisée, contenant une grande quantité de noyaux de même forme et de même structure, traversée par quelques capillaires volumineux. Figs. 1, 2, 5 et 6. Durant le développement embryonnaire, la plasmodie hépatique se scinde en de multiples éléments, de nombreuses cellules, parmi lesquelles des cellules sanguines.

(2°) Les noyaux hépatiques que l'on observe presqu'exclusivement durant les premiers temps présentent des figures de division mitotique assez nombreuses.

Ils s'entourent d'une zone protoplasmique éosinophile, qui se détache du restant de la plasmodie. Il se forme ainsi des cellules isolées, soit au niveau de grandes vacuoles, soit dans le voisinage immédiat des grands capillaires.

Ces cellules se détachent de la plasmodie et vont constituer des cellules sanguines. Figs. 1, 3, 4, et 6.

Les phénomènes de division nucléaires dans les cellules sanguines devenues intravasculaires continuent à se produire, fig. 1 *V*, à l'intérieur des vaisseaux.

(3°) On peut distinguer trois périodes d'activité dans la formation des cellules sanguines dans le foie embryonnaire:

(*a*) Une période *d'activité lente* qui s'observe chez l'embryon de lapin jusqu'au 11me jour. Figs. 1 à 6.

(*b*) Une *période intermédiaire* qui dure peu, quelques jours seulement, jusqu'au 14me jour ou à proximité de cette date.

Durant cette période les divisions sont un peu plus nombreuses, et les cellules qui en proviennent sont un peu plus petites. Fig. 7.

(*c*) *Une période de grande activité*, à partir du 14me ou 15me jour, forme une troisième période qui se caractérise par la production de cellules sanguines très nombreuses, sensiblement plus petites, à noyaux présentant successivement des phénomènes de division *mitotique* et *amitotique*. Figs. 8, 9 et 10. Les noyaux en division amitotique sont généralement formés par une masse nucléaire sans structure bien définie, colorée intensément par les colorants nucléaires. Les nouveaux noyaux paraissent être en état de *pycnose*. On en voit à la périphérie des cellules, prêts à être expulsés; dans d'autres cellules sanguines la région du noyau n'est plus que très faiblement colorée par les colorants nucléaires. Figs. 11 et 14. Il est nécessaire d'observer ces trois

périodes pour l'étude de l'origine des cellules sanguines dans le foie embryonnaire. L'étude de la 3me période de grande activité ne suffit pas.

(4°) Les cellules géantes qu'on observe dans le foie dès le 14me jour semblent avoir la même origine hépatique. Ce sont de grandes masses protoplasmiques découpées dans le plasmodie et contenant un certain nombre de noyaux, qui se fusionnent plus ou moins.

(5°) L'origine hépatique, c'est-à-dire hypoblastique, des cellules sanguines de l'embryon n'est pas la seule qu'on puisse observer. Elle n'est probablement que transitoire, passagère, n'existant qu'à une certaine période du développement de l'embryon.

LOUVAIN,
Novembre, 1925.

"Semper aliquid novi ex Africa"

A CONTRIBUTION TO THE MORPHOLOGY OF THE THUMB

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INTRODUCTION

The anatomical pebble to which unsuspecting Galen gave an impetus nearly two thousand years ago has not yet ceased to roll. Unlike another stone famed in metaphor, this one has gathered moss and to spare. The literature concerning the thumb probably surpasses in extent that dealing with some organs of greater import. The most rational excuse for adding still further to a plethora will be found in the case herewith reported and commented on.

The writer was medical officer to the City Deep Central Native Hospital. This is the largest of its kind on the reef and comprises almost four hundred beds. While occupying this position, a case of abnormality of the thumbs was encountered, which is probably unique. The patient was an East Coast native belonging to the Shangaan tribe. He possessed not only three phalanges on each thumb, but also a well-formed accessory thumb, with two phalanges, on the left hand. The unusual nature of the case suggested this research into the morphology of the thumb. The paper deals mainly with the thumb, the great toe is belaboured but little.

Thanks are due to A. J. Orenstein, for permission to use the material at the City Deep Central Native Hospital; to Professor Raymond Dart for much helpful advice in the preparation of this paper, and for the use of the material in the dissecting room of the Department of Anatomy; to Dr Laing, Senior Lecturer in the same department, for the use of fig. 7; and to Mr Le Helleco, Student Demonstrator of Anatomy, for the drawings in figs. 6 and 7.

The communication is arranged in the following order:

(1) The description of the case.
(2) The X-ray appearances of the hands in this case.
(3) Brief outline of the literature regarding the morphology of the thumb.
(4) Constitution of the terminal phalanx of the thumb, including
(5) A critical survey of the variations in the attachments of the extensors of the thumb, introducing

(6) The extensor brevis digitorum.
(7) The ossification of the first metacarpal.
(8) Summary.

DESCRIPTION OF THE CASE

Adult male native, aged forty, admitted to the City Deep Central Native Hospital under the writer's care, suffering from lues.

Left hand. There were two thumbs present, the one in the normal situation possessed three phalanges, the second jutted radially at right angles from the region of the head of the metacarpal and had two phalanges. The thumb with three phalanges was longer than a normal thumb; it had a slight deflection ulnarwards instead of the normal radial deflection.

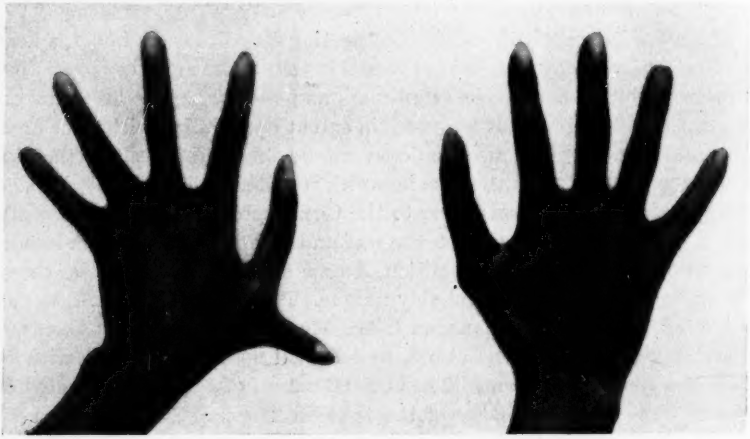

Fig. 1. Demonstrates the appearances seen from the dorsal aspect in the hands of the case described.

This digit showed an interesting feature in the appearance of the skin over the dorsum of the inter-phalangeal joints (see fig. 2), i.e. that over the first inter-phalangeal joint possessed the normal creases seen in that situation in the thumb; the skin over the second inter-phalangeal joint was smooth with slight creasing.

Does this indicate that the morphological first inter-phalangeal joint has persisted in relation to the skin area which has the typical appearance present over the first joint, and that the joint is therefore situated between the first and second phalanges to-day, the second one being represented by the base of the distal phalanx? The thumb possessed a normal degree of movement both as regards strength and range.

Accessory thumb. This projected at right angles from the head of the metacarpal. It had two phalanges and looked a perfectly normal thumb excepting that it was a little smaller. The nail was normal in size, position

and formation. Movement appeared to be free, but on examination was found to be mainly due to the movement of the metacarpal. Flexion was strong, and was due to a process from the long flexor going to the terminal phalanx. There was some movement at the metacarpo-phalangeal joint; there was creaking in the joint suggesting arthritic change, but the movement was quite painless. The movement at the inter-phalangeal joint was limited. The thumb received a slip to the terminal phalanx from the extensor pollicis brevis. This is well shown in fig. 3 where the boundaries of the anatomical snuff box are seen to be parallel and not converging as is usually the case.

Fig. 2. A closer view of the two thumbs present in the left hand. Note the skin markings over the normally situated thumb, also the normal appearance of the accessory thumb. The perfect formation of the nail is well shown in this and the next figure.

This is accounted for by the fact that the short extensor is pulled radially by the slip to the accessory thumb. No short muscles were attached to this digit. The patient worked underground; the condition of his hands inconvenienced him in no way.

Right thumb. This digit possessed three phalanges; there had never been an accessory digit on the right hand. The thumb was considerably longer than the left main thumb. The right thumb and the left main thumb both resembled fingers rather than thumbs. There was none of the spatula appearance of the thumb but rather a tapering like that of the finger. It is worth

mentioning that the terminal phalanx in the thumbs of natives, although long, is relatively slender. Frequently also, the second phalanx, when fully extended, forms wholly, or not quite, a straight line with the first phalanx. This may doubtless be correlated with the fact that members of the Bantu race are not craftsmen, and that most of the manual work is done by the womenfolk.

Family history. It is usually impossible to obtain this from a Kaffir. Fortunately this individual was an exception. His paternal grandfather's hands were exactly comparable with his own. He had had six brothers in all, two alive, four dead. In all there existed three phalanges in each thumb but no accessory digits. There had been only one mother; her hands were normal. He knew of no other congenital abnormalities in any member of the family; he had no sisters. He had no children of his own. This case is further evidence of the hereditary nature of abnormalities of the digits.

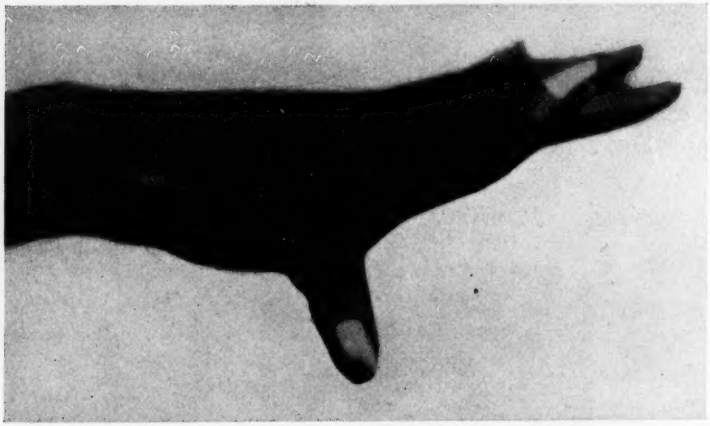

Fig. 3. The left hand seen from the radial aspect. Note that the boundaries of the anatomical snuff box are parallel.

X-RAY APPEARANCES

These are demonstrated in figs. 4 and 5.

The left first metacarpal is normal in length and architecture except for a stout rounded projection from the radial side of the distal end. This is an instance of dichotomy of the head of the metacarpal. The left main thumb possesses three phalanges. The first is normal. The second is unduly short, in fact the shortest of the three. The distal phalanx is shorter than normal and resembles the distal phalanx of a finger in length (*vide infra*). The metacarpo-phalangeal joint of the accessory thumb resembles a normal joint of this nature, and not an inter-phalangeal joint. Notice the shape of the bone ends. Therefore the projection from the radial side of the first metacarpal is not a

first phalanx, but represents the second head of a metacarpal which is bifid at its distal end. The first phalanx is shorter than the second, being an accessory digit, but little can be deduced from this.

Right first metacarpal. This bone resembles a finger metacarpal in its length and slenderness. The phalanges are similar to those described for the corresponding left digit.

Fig. 4. X-ray antero-posterior view of the left hand. Note the length of the second phalanx of the normally situated thumb, the ulnar deflection of the phalanges and the accessory thumb.

A BRIEF REVIEW OF THE LITERATURE REGARDING THE MORPHOLOGY OF THE THUMB

The divergence of opinion concerning the morphology of the thumb, expressed by various writers, denotes the undecided state of knowledge on the subject.

Nearly two millennia have passed since Galen expressed the opinion that the first metacarpal represents the first primitive phalanx because of its

anomalous method of ossification. The direction of the nutrient canal has more recently been adduced as evidence in favour of this conclusion.

Gegenbauer held the view that the first metacarpal is the true middle hand bone; that is to say, it corresponds morphologically to the middle segment of the skeleton of the hand; the carpus representing the proximal, and

Fig. 5. X-ray antero-posterior view of the right hand. Note again the second phalanx of the thumb. Compare the thumb metacarpal with the other metacarpals and with the first metacarpal in fig. 4.

the phalanges the distal segment. He based his opinion on the relationships of the thumb muscles. Welcker and others supported this view. Further evidence in support of this theory was supposed to be found in the occasional appearance of a distal epiphysis to this metacarpal, as also in the rare occurrence of three true phalanges appearing in this digit. Such cases have been reported from time to time. The name of Kirmisson is noteworthy in this connection. Uffelman, again, was of opinion that the first metacarpal

was constituted by a fusion of metacarpal and first phalanx. Approaching the problem by way of skiagraphy Harris concludes that the middle phalanx is suppressed. He bases his contention on the order of appearance of the centres of ossification.

McFarland in his *Surgical Pathology*, published in 1924, states, that during development, there are as many bony elements in the thumb as in the other digits, but that the reduction is effected by the fusion of the first metacarpal with the first phalanx. He quotes Sappey to the same effect. The occasional occurrence of three phalanges in the thumb is ascribed by him to an arrest of development before fusion takes place. He refers to many of Kirmisson's cases which are described in *Traité des maladies chirurgicales d'origine congénitale*. The consideration of these divergent views leads Wakeley to conclude that Gegenbauer's idea of the morphology of the thumb is the correct one. So too he agrees with Pfitzner's explanation of the reduction in the number of phalanges in the thumb. (This observer stated that the original second and third phalanges have fused to form the present distal or second phalanx.) The work done in the course of this investigation favours overwhelmingly the theories of Gegenbauer and Pfitzner regarding the manner of constitution of the different thumb bones. Therefore according to the work done here Wakeley's conclusions are correct. The nature of the distal phalanx is considered first.

CONSTITUTION OF THE DISTAL PHALANX OF THE THUMB

This phalanx is built up by both the second and third primitive phalanges. This being so then the first phalanx morphologically represents the first primitive phalanx, and cannot therefore be fused with the first metacarpal. Evidence in support of this view of the constitution of the last phalanx is forthcoming in considering

(*a*) the relative lengths of the thumb phalanges in the normal hand;

(*b*) the relative lengths of the thumb phalanges in the hands described and figured in this case;

(*c*) the variations in the attachments of the thumb extensors.

Each of these points will be considered separately.

Relative Lengths of the Thumb Phalanges in the Normal Hand.

Examination of skiagrams of normal adult hands shows that, in the great majority of cases,

(1) The proximal phalanx of the thumb is shorter than the proximal phalanx of the other digits.

(2) The proximal phalanx of the thumb is usually but little longer than its own terminal one.

(3) The terminal phalanges of the other digits are less than half the length of their corresponding proximal phalanges.

(4) The terminal phalanx in the normal thumb is longer both relatively and absolutely than the terminal phalanges in the fingers.

This apparently disproportionate length of the distal phalanx of the thumb would seem to show quite obviously that it is different from the distal phalanges of the fingers and that the most likely explanation of this is that it is built up of two bones. Why otherwise should the ungual phalanx of the thumb possess the features tabulated above?

Relative Lengths of the Phalanges of the Thumb in the case described

In the thumbs (excluding the accessory one) of this abnormal case a well-developed first phalanx is seen. The second phalanx is remarkably short, while the terminal one is only half the length of the corresponding first phalanx. It will be found on comparing this with the normal, that the terminal thumb phalanges in this case are considerably reduced in size when compared with their own first phalanges, and are comparable in length with the last phalanges in the fingers: that is to say, the terminal phalanges of the thumbs in this case resemble the terminal phalanges in the fingers and are shorter than the last phalanges of a normal thumb. In a normal digit the bones decrease in length from the metacarpal proximo-distally. This however is not the case in the thumbs shown in figs. 5 and 6 (excluding the accessory one) as the second and not the terminal phalanx is the shortest of the three. The writer believes that here lies the secret of the great size of the last phalanx in a normal thumb. It represents a fusion of the second and third primitive phalanges. This case would then typify a reversion to some ancestral type where the second phalanx is undergoing shortening. A reconstruction of the successive morphological stages, shows, that the second phalanx has decreased progressively in length in phylogeny, and has ultimately fused with the base of the terminal one. In this way is produced, paradoxical as it may seem, an abnormally long terminal phalanx in the thumb which is normal none the less. Here then is the explanation of the relatively greater length of the terminal phalanx of modern human thumbs as compared with the terminal phalanges of the fingers. The modern ungual phalanx of the thumb is a composite bone comprising both second and third primitive phalanges.

Since these conclusions seem justifiable, it was thought that the variations in the attachments of the thumb extensors would support them. An analysis was therefore made of the attachments of these muscles in members of the great Bantu race, comprising individuals of the Basuto, Shangaan, Pondo, Bechuana and Makalaka tribes.

VARIATIONS IN THE ATTACHMENTS OF THE EXTENSORS OF THE THUMB

It is a reasonable assumption that when the thumb had three phalanges it possessed one or more long extensor muscles. Arguing by analogy with the fingers, their tendons were most probably attached to the second and

third phalanges with an expansion over the first phalanx similar to that existing over the first phalanges of the fingers (*vide infra*). If such be the case the extensor pollicis longus tendon represents the long lateral slips of the extensor apparatus which gain attachment to the last phalanx. Contrariwise the extensor pollicis brevis tendon represents the short central slip which is attached to the base of the second phalanx of the fingers. One would expect therefore that the extensor pollicis brevis would be attached to the base of the second or terminal phalanx of the thumb (this being the representative of the second primitive phalanx) but the usual anatomical description is that it is attached to the base of the proximal phalanx, which is (according to the

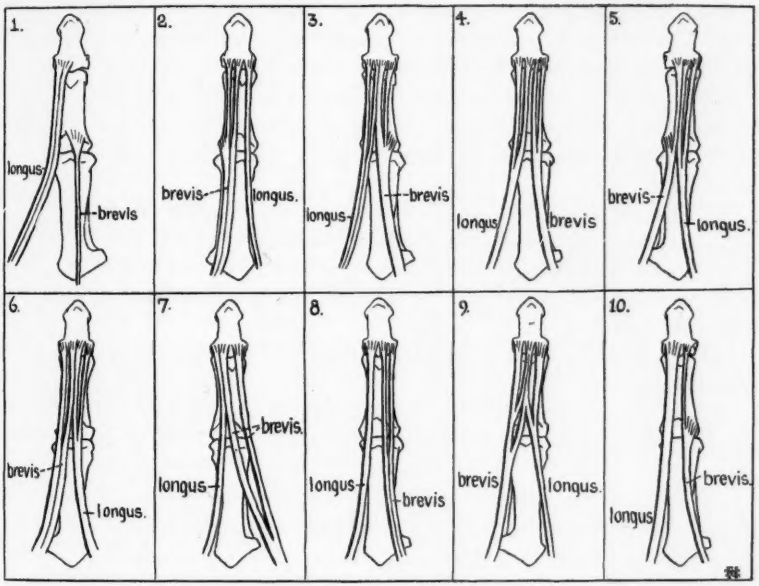

Fig. 6. Illustrates some of the variations of the manner of termination of the extensors of the phalanges of the thumb.

view held by the writer and others) the morphological representative of the true first phalanx. Investigation of one hundred hands in members of the Bantu race has shown that it is attached to the base of the proximal phalanx in only 5 per cent. of cases. It is found in these races that the tendon of the extensor pollicis brevis is attached to the base of the terminal phalanx in the vast majority of cases instead of being attached to the proximal one. What then are the facts about the extensor pollicis brevis muscle? Cunningham and Gray both state that the tendon of this muscle ends at the base of the first phalanx. Morris quotes Le Double who found a slip from this tendon to the first metacarpal in two out of eighty-five bodies. It is stated by Piersol and the authors cited that a slip may occasionally be continued to the terminal

phalanx. Werner Spalteholtz makes no reference in his *Atlas* to a possible continuation of the tendon. Frohse, in his account of this muscle, states that it is a demarcated portion of the abductor pollicis longus, and that its insertion is usually on and in the capsule of the metacarpo-phalangeal joint; also that the tendon can often be followed to the terminal phalanx. The features of the extensor tendons have been investigated in one hundred Negro hands.

Part were examined in a large native hospital at the time when a post mortem was performed. Others were examined in dissecting room subjects. All these hands belonged to members of the great Bantu race of Kaffirs.

The following facts have emerged:

(1) The extensor pollicis brevis continues in whole or in part to the terminal phalanx in the vast majority of cases.

(2) In only 5 per cent. of cases did this tendon terminate at the base of the first phalanx. In these cases the tendon was abnormally small, much smaller than the tendon of the long extensor. The tendon was expanded at its insertion.

(3) The relative thickness of the tendons varied greatly, sometimes the short extensor was the larger of the two, sometimes the opposite obtained.

(4) In all cases the two extensors were intimately related to the dorsal ligament of the metacarpo-phalangeal joint, and it was difficult or impossible to dissect them from it.

(5) The tendons were frequently divided into two on the dorsum of the metacarpal.

(6) In no case was there an interchange of fibres between the tendons over the metacarpal. From the metacarpo-phalangeal joint onwards the two tendons were often inextricably blended.

(7) In many cases there was a strong dorsal expansion over the back and sides of the first phalanx. This was exactly comparable to that over the first phalanx of the other digits (*vide supra*). The short volar muscles were partly attached to this aponeurosis.

Taking the facts enumerated above in conjunction with the facts concerning the extensor pollicis brevis in the European subject one is led to believe that the extensor pollicis brevis tendon is migrating to the base of the first phalanx from its primitive attachment to the base of the second one. These facts are in favour of the fusion theory as explaining the constitution of the terminal phalanx of the thumb. The extensor pollicis brevis is shifting its attachment to the base of the proximal phalanx as it is no more required to extend the second primitive phalanx which now forms part of the modern ungual phalanx. This discrepancy regarding the extensors of the thumb which exists between the facts enumerated above and the text-book description is due no doubt to the subjects from whom the respective data were forthcoming. Primitive features such as abnormal muscles, etc., are far more frequent in natives than in whites. The former frequently present features

which are of great value in elucidating the history of such muscles, etc. From these facts relating to the extensor brevis it is reasonable to believe that the present first phalanx represents morphologically the first phalanx; were it the case that the first phalanx had fused with the metacarpal, one would expect to find the short extensor of the thumb attached more constantly to the base of the present first phalanx, which would then represent the second phalangeal element. (Consequently Welcker's theory that the present first phalanx is morphologically the second is not borne out by the study of the attachments of these muscles in primitive peoples.) A discussion of the view of Welcker and others, that the extensors of the thumb are portions of the communis extensor is not relevant to this article. Reference will however be made to a muscle which the writer has labelled the *extensor digitorum brevis*. If this name has been applied to it before he is not cognisant of the fact.

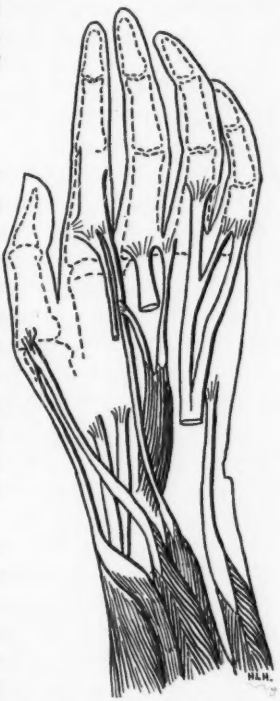

Fig. 7. Extensor digitorum brevis found in dissecting room subject. It divides into two slips, one of which goes to the tendon of the extensor indicis proprius, the other goes to one of the slips of the communis.

THE EXTENSOR BREVIS DIGITORUM

This muscle has been found in four different cases. Three occurred in the cadaver and one in the living subject; all the cases occurred in Bantu men. The cases seen in the dissected subject were uni-lateral. The muscle is short, flat and triangular. It arises on the dorsum of the hand from the region of the dorsal carpal ligament or from the dorsum of the metacarpus. It expands as it is traced distally and lies between the extensor tendons and the bones. It divides into two or three tendons which are attached to the long extensor slips going to the radial two or three fingers.

In the case figured (fig. 7) one of the two slips is given to the tendon of the extensor indicis proprius.

One of the muscles was discovered while operating on a native who had had the tendons cut on the dorsum of the hand. An unusual number of tendon ends was found. Some of these belonged to the processes of a powerful extensor brevis digitorum. Although the muscle has not been found to give a slip to the extensor pollicis longus tendon, it is mentioned nevertheless as a possible explanation of the fact that the tendon of this latter muscle is frequently divided into two portions. May not the tendon of the extensor pollicis longus have absorbed a slip from a one-time muscle

on the dorsum of the hand of which the extensor brevis digitorum occasionally reminds the anatomist? The condition would then be analogous to that which obtains in the extensors of the great toe.

To summarise

The distal phalanx of the normal thumb represents the product of the fusion of the second and third primitive phalanges. This conclusion is supported firstly by the absolute and relative length of the phalanges in the normal thumb compared with those in the fingers; secondly by the characters of the phalanges in the case depicted; and thirdly by the facts elucidated in regard to the attachments of the thumb extensors.

THE OSSIFICATION OF THE FIRST METACARPAL

Any discussion of the morphology of the thumb would be incomplete without reference to the ossification of the first metacarpal bone. Allusion has already been made to the excellent work on ossification which was done by Harris with the assistance of radiography. The whole subject of ossification is wrapped in obscurity. This is especially the case when the epiphyses are considered. Why should one bone have numerous secondary centres, while another quite as complex in structure has none? This and many other facts in connection with ossification remain at present unexplained. The writer is firmly convinced that the position and times of appearance and fusion of epiphyses are governed by definite natural laws. The views on ossification expressed below will be amplified in a paper now in course of preparation. How then is one to explain the aberrant character of the ossification of the first metacarpal and the first metatarsal? Any observer is struck by the great purpose which runs through Nature. There is always economy of effort, and an explanation of some seemingly inexplicable fact, even though that explanation may not be to hand. There must be some reason for the fact that the epiphyses of the first metacarpal and the first metatarsal are at the base and not at the head. In trying to find this explanation the occasional existence of an epiphysis for the head must be borne in mind. In comparing the maxilla with the fibula in their method of ossification, it is noteworthy that the fibula has three centres, the maxilla but one (excluding the pre-maxilla). The maxilla is much more complex in its contours than the fibula. Why this seeming lavishness of effort? It appears that a consideration of the joints may supply this explanation. The fibula assists in the formation of two diathrodial joints, the maxilla in none. All the long limb bones have at least one epiphysis at each end. All the long limb bones participate in complex diathrodial joints. Surely here lies the explanation of this profusion of ossific centres. When the short long bones are considered the economy of effort is realised. They have but one epiphysis as a rule. The underlying plan may be stated as follows:

(1) The long bone ends participating in diathrodial joints are in all cases epiphyses.

(2) In every diathrodial joint at least one of the joint surfaces is an epiphysis (a small bone may be regarded as an epiphysis).

(3) In the short long bones the more freely moving bone end is the epiphysis.

All great bridges are built according to the same basic laws of engineering and mathematics. In the joints between the girders room is left for the expansion produced by changes of temperature. A working margin is required where alterations due to changing conditions can be accommodated. It seems that epiphyses, or rather the situations at which epiphyses appear in a bone, are to be explained in a similar way and have a mechanical rather than a morphological explanation. Epiphyses are Nature's working margin. As no two faces are alike, so doubtless, no two joints are exactly alike. The alignment of the bones, the lines of stress, are gradually perfected; the epiphyses are areas of relative elasticity, where slight changes in direction can be made to suit the needs and environment of the individual. A protected adolescence or a blusterous one produces equally perfect joints. Bandy-legged people do not normally develop arthritis in the joints of the lower limbs, although the bones are thrown out of alignment. There must be a working margin where the small adjustments necessary to produce a perfect mechanism can be effected—the epiphyses. (By an epiphysis is meant the whole structure on the epiphyseal side of the metaphysis.) The typical site of appearance of the epiphysis in the first metacarpal bone can be explained rationally on mechanical lines. All efforts at explaining the method of ossification of this bone merely by comparison with the other metacarpals, lose sight of the total difference in the nature of the joints at their respective proximal ends. The explanation must be sought in the mechanics of these joints. The range of movements at the carpo-metacarpal joint of the thumb is more extensive than at the metacarpo-phalangeal joint. Therefore the epiphysis has evolved at the base of the metacarpal. The bones participating in the first carpo-metacarpal joint are moulded on a complex ephippial pattern. They must co-apt perfectly. The base of the metacarpal is an epiphysis where constant small changes can be effected until the mechanical harmony of the articulation in relation to the stresses to which the particular joint is subjected is perfected. It may be that at some previous stage of evolution the opposite obtained, hence the atavistic appearance of centres for the head of the first metacarpal and metatarsal. The second to the fifth metacarpals and metatarsals have simple arthrodial joints at their bases; they take part in freely moving distal joints, hence the epiphysis is at the head of the bone. It is here that accurate co-aptation is necessary and here complex surfaces come into inter-relationship. The phalanges move on the metacarpals, the distal ones move on the proximal ones, therefore the epiphyses appear at the bases. The freely moving bone has a give and take area (the epiphysis) where alterations can be accomplished

to perfect the relationship of the joint surfaces and the shape of the bone. The tarso-metatarsal joint of the great toe may appear an exception, but if the apposable hallux of the great apes be considered, it will be seen that the tarso-metatarsal joint corresponds to the carpo-metacarpal in freedom of movement. Perhaps the orthograde posture may result in a shifting of the epiphysis of the first metatarsal to the more mobile phalangeal end of the bone at some distant geological epoch. It will therefore be seen that the difference between the ossification of the first and following metacarpal bones (the same applies to the metatarsal) is explicable on purely mechanical lines. Efforts, such as those of all previous workers, to explain the ossification on purely morphological lines are fraught with failure from their inception. Leaving the thumb for a moment, are these laws of ossification found to be of general applicability? The writer believes they are, although their applicability may not as yet be patent in regions where morphology is unelucidated. The centres for the skull bones and for the scapula are difficult to explain, but a more exact knowledge of the stages in their evolution may bring even these into line. The laws formulated above apply to bones which have to bear weight or which are being constantly subjected to powerful muscular action. Why does a secondary centre appear at the sternal end of the clavicle at the age of eighteen? May not the reason be that about this age the upper limbs approach full development and the serious and often laborious period of life begins? Until the time of fusion of the inner end of the clavicle with the shaft there exists an area where the direction of the joint surface in relation to the articular disc can be altered as may be necessary until the position of maximum advantage is obtained.

SUMMARY

(1) An abnormal case is described and illustrated. In this case both thumbs possessed three phalanges, the second of which was the shortest. Appended to the left first metacarpal was a well-formed accessory thumb possessing two phalanges.

(ii) From this case and from the relative lengths of the phalanges of normal thumbs evidence is adduced in support of the contention that

(iii) The first metacarpal morphologically represents the first metacarpal only. The proximal phalanx is the proximal phalanx only. The distal phalanx represents the product of the fusion of the second and third primitive phalanges.

(iv) The extensor tendons of the thumb in the native are analysed with regard to their modes of insertion and brought forward in support of the fusion theory of Pfitzner, mentioned in (iii).

(v) The peculiar method of ossification of the first metacarpal (also the first metatarsal) can be adequately explained by mechanical reasons only.

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THE COURSE, MUTUAL RELATIONS AND DISTRIBUTION OF THE CUTANEOUS NERVES OF THE METAZONAL REGION OF LEG AND FOOT

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INTRODUCTION

The reason for this research is the great variation in the distribution of the cutaneous nerves of the leg and foot observed by the author in the dissecting room and in the course of several personal dissections, and the aim of this work is to establish the types of variations met with. Owing to the strange variation in the course of usually constant and recognised nerves the author must claim only a relative value for the results of his work. If one could but establish the relative rules of the course and mutual relations of the cutaneous nerves of the leg (which are described in such different manners by the authors of the classical text-books) so as to bring us nearer to the anatomical and anthropological truths, the work would be justified.

It is sufficient to compare the description concerning the nerves of the calf in the most classical text-books of descriptive anatomy to justify the above statement. I refer especially to the text-books of Cunningham (ed. 1922, pp. 760–762), Gray (22nd ed. 1923, pp. 963–965) and Quain (11th ed. 1909, vol. III, pp. 112–115) in England, to those of Morris (6th ed. 1921, pp. 1043–1047–1048), Gerrish (ed. 1899, pp. 629, 633, 636) and Pearsol (ed. 1919, pp. 1336–1342) in America, to those of Testut (6th ed. 1921, vol. III, pp. 227–228–233–234), Gerard (2nd ed. 1921, pp. 692–693) and Poirier et Charpy (1921, I et II fasc.) in France, and to those of C. Gegenbaur (2nd ed. pp. 910, 912, 913), Rauber-Kopsch (5th ed. 1898, 2nd vol. pp. 548, 549, 552) and Henle (4th ed. 1901, pp. 520–522) in Germany and I. Romiti (1899, vol. II, pp. 875–878) in Italy. Space forbids quotation of the above somewhat long extracts. In my opinion the most correct description is that given by Cunningham.

With regard to cutaneous innervation, the posterior surfaces of the thigh and leg and the dorsum of the foot form a certain unit whose boundaries have already been defined by M. Fürbringer (7).

This region was called by this author the "Metazonal" region of the cutaneous distribution of the nerves of the lower extremity and its boundaries are as follows:

(*a*) Medial boundary line—from the mid-point between medial malleolus and tendo Achilles it ascends upon the medial head of gastrocnemius in a straight line to the medial border of popliteal space and then along posterior border of gracilis to the external genital organs.

(*b*) Lateral boundary line—from the great trochanter it descends along biceps to lateral side of knee-joint in a straight line and then in a spiral line it crosses the anterior surface of the leg to reach the anterior border of medial malleolus.

These two boundary lines subdivide the lower limb into a metazonal (posterior) and a prozonal (anteromedial) region; the cutaneous supply of the metazonal region is derived from the sacral plexus and that of the prozonal region from the lumbar plexus. L. Bolk in 1897 (2) as regards both regions. and G. Ruge in 1893 (14) as regards the prozonal region only, treat the cutaneous innervation of the lower limb in anthropoids from the point of view of its development, whereas Fr. Leuzzi in 1904 (11) (as regards the innervation of the calf) and V. Catania recently in 1924 (3) (especially as regards the innervation of dorsum of foot) treat this question from the anatomical and anthropological points of view. The Committee of Collective Investigation of the Anatomical Society of Great Britain and Ireland was the first to apply the statistical method (in 1890 and 1891) to investigate the question of the innervation of dorsum of foot: 226 cases were examined (see (13)). Fr. Leuzzi dissected about 40 human legs and several animals, and V. Catania 100 human legs.

The author commenced his work with no knowledge of Leuzzi's work (this latter work being published unfortunately in purely biological periodicals not usually read by medical people) and coincident with that of Catania who published his results in September 1924.

The author has not hitherto published the results of his investigation, which was completed in March 1924.

The variation in the formation of the sacral plexus throws some light upon the variation in the cutaneous nerve supply of the leg and foot (1).

The theory established by Bolk in anthropoids that the more distal nerves tend to occupy the regions previously innervated by more proximal nerves, can be kept in mind even if not strictly true, because it throws some light on the question of the variability of the cutaneous innervation and thus justifies its existence. This theory not only enables us to comprehend all the variety of distribution of the nerves, but also the differences in different races, which, if established will be very important to anthropology.

What factors influence the variation in the formation of the sacral plexus? This question is difficult to decide. It may be due to the process of shortening of the trunk in higher mammals, especially in man, as well as the simple displacement of the origin of the limb-buds in a caudal or cephalic direction. Perhaps both these factors act simultaneously.

Undoubtedly some nerve fibres pass from one nerve to another and this is not the result of a mere accident. From embryology and comparative anatomy we know that all variations have a deeper developmental origin, and we must therefore give proper attention to any anatomical changes.

As regards the innervation of the metazonal region of the lower extremity

we must remember the order of emergence of the nerves from the sacral plexus which is as follows going from the proximal (cephalic) to the distal (caudal) nerves:

1. Common peroneal nerve. L iv–S ii (*a*) deep peroneal nerve, (*b*) superficial peroneal nerve.
2. Tibial nerve. L iv–S iii.
3. Small sciatic nerve. S i–S iii.

The deep peroneal nerve, which supplies the extensor muscles, is more proximal than the superficial peroneal nerve, which supplies the peroneal muscles (longus and brevis) which occupy the lateral (caudal or distal) border of the leg, and the topographical position of the nerve, as regards the segmental innervation of the limb, is fixed to some muscles, and this decides the innervation of the cutaneous area of that nerve. Comparing the distribution of the cutaneous nerves of the metazonal region in anthropoids and man we note the following:

1. The saphenous nerve (derived from the anterior crural L ii, iii, iv) in anthropoids is continued to the top of the great toe (medial side), whereas in man it only extends as far as the medial malleolus, and the lost area is supplied by the more distal superficial peroneal nerve.
2. The deep peroneal nerve in anthropoids supplies the skin of the medial side of the 2nd toe and the adjacent sides of the 2nd, 3rd and sometimes even the 3rd and 4th toes, whereas in man this area is displaced medially and restrained and the nerve supplies only the adjacent sides of 1st and 2nd toes. The lost area is innervated by the more distal superficial peroneal nerve.
3. The superficial peroneal nerve in anthropoids supplies the adjacent sides of the 4th and 5th toes and sometimes the lateral side of the 5th toe as well as the contiguous sides of the 1st and 2nd toes, whereas in man this area is displaced medially and enlarged and supplies the medial side of the 1st toe, and adjacent sides of the 2nd, 3rd and 3rd and 4th and sometimes 4th and 5th toes. The lost area in man is supplied by the more distal dorsal cutaneous nerve (sural nerve). This last nerve in man often enlarges its distribution in a medial direction even as far as the adjacent sides of the 3rd and 4th toes.

Material and Method of Research

Author has dissected 118 legs as follows:

	Sex	Right side	Left side
Male	66	32	34
Female	48	25	23
Unknown	4	2	2
Total ...	118	59	59

and about 50 different animals (mammals) in the Zoological Gardens of London.

The length of the leg was measured in the usual anthropological way from the level of the knee-joint on the medial side (the medial condyle of tibia being the bony landmark) to the tip of the medial malleolus (sphyrion).

The great sciatic nerve was found to divide on an average 10·2 cm. above level of knee-joint (approximately at junction of 3rd and lower quarters of thigh).

Range 3–16 cm.; most common: 8 cm. in 18 cases; 10 cm. in 32 cases; 12 cm. in 33 cases.

The figures are in agreement with the theory of Rosemuller who states that the great sciatic nerve in northern races divides at a higher level than in southern races (see Caetano Cutore 1901(5)). Ancel in Lothringen—60 % of high division (1900), Calori in Bologna—26 % (1880), Legge in Cagliari—6 % (1896), Cutore in Catania—15 % (1901). Quain and Gegenbaur—in the middle of the thigh (most common division).

In the dissected mammals we found the division at a higher level than in man, on an average somewhat below the middle of the thigh and the nerve was easy to separate in the upward direction.

Topography of Popliteal Space

Greatest transverse diameter is placed on average about 3·4 cm. above knee-joint.

Superior angle. 10·4 cm. above knee-joint and corresponds to position of bifurcation of great sciatic nerve.

Inferior angle. Level of knee-joint line; this relation may be important in operations in that region when it is otherwise difficult to establish the line of the knee-joint.

The distance between the tibial and common peroneal nerves at the level of the knee-joint is on average about 3 cm. (range 2–3·5 cm.). This relation is useful in operative surgery owing to the changeable position of the common peroneal nerve, the tibial nerve being constant in the median position.

The following work is divided into two parts.

Part I deals with the cutaneous innervation of the metazonal region of the leg, and begins with the most distal small sciatic nerve and ends with the most proximal lateral sural nerve.

Part II deals with the cutaneous innervation of the metazonal region of the foot beginning with the most distal lateral dorsal cutaneous nerve and ending with the most proximal deep peroneal nerve.

PART I

CUTANEOUS NERVES OF THE CALF

1. Small Sciatic Nerve. (N. cut. femoris posterior)

This descends to a lower level than described in some text-books (Henle, Gegenbaur). Generally it terminates in the middle of the leg, sometimes it descends even as far distally as the heel and exceptionally it ends in the region of the knee-joint.

Table of extent of small sciatic nerve:

(i)	To level of knee-joint	5·5 %	(6 cases)
(ii)	Proximal quarter of leg	22·7	(25 ,,)
(iii)	Second quarter of leg	33·6	(37 ,,)
(iv)	Third quarter of leg	30·9	(34 ,,)
(v)	Distal quarter of leg	7·3	(8 ,,)
	Total ...	100 %	110 cases

In other words the average descent is between 40 and 60 % of the length of the leg (below the level of the knee-joint). To this number must be added about 5·10 % on account of the possibility always present of imperfect dissection of the very small terminal branches (see figs. 5 and 8). This lower descent of the small sciatic nerve has been described by L. Bolk also in anthropoids (2). The small sciatic nerve (as above described) always accompanies the small saphenous vein in the leg, usually (in 73·7 %) lying on the medial side of the vein, and therefore runs in the median line of the leg. The vein and nerve lie in the same fascial plane and in the same fascial space, which shows that the nerve supplies the skin of the median and somewhat more medial parts of the posterior surface of the calf in the proximal half of the leg. The median sural nerve (medial sural cutaneous nerve) in the proximal half of the leg lies below the deep fascia and does not give off any cutaneous branch. The area supplied by the small sciatic nerve is contiguous to that supplied by the great saphenous nerve (which lies on its medial side) and to that of the lateral sural (cutaneous) nerve (which lies on its lateral side). The lateral sural nerve is in clear compensatory relation with the small sciatic nerve (see subjoined figures) the compensatory value being especially evident in the rare cases of complete absence of the lateral sural nerve where the branches (especially lateral) of the small sciatic nerve are unusually large and numerous (figs. 7 and 8).

2. The Median Sural Nerve. (Medial sural cutaneous nerve, B.N.A.)

General Characteristics. This nerve arises from the tibial nerve on an average about 8 cm. above the level of the line of the knee-joint. Its course on the back of the leg is quite deep, between the two heads of the gastrocnemius muscle,

especially in the middle third of the calf where it may (in 40 % of the cases examined) lie on the posterior surface of the *soleus* muscle even. It pierces the deep fascia of the leg about 62 % (2/3) of the distance from the knee to the heel and usually gives off its first cutaneous branches in the distal fourth of the leg; it also constantly supplies lateral cutaneous branches to the heel. Thereafter in 53·8 % it descends on the dorsum of the foot as the lateral dorsal cutaneous nerve.

Only in 40·2 % of the 118 legs dissected did the nerve receive an anastomotic branch from the lateral sural nerve to form the generally described sural nerve. (This latter arrangement has been regarded as the rule with few exceptions). This formation of the sural nerve is confined to man and is not found in animals, even in anthropoids; the lack of anastomosis between the nerves (as above described) must be regarded as a reversion to the state in anthropoids. Perhaps the arrangement varies in different communities, possibly as the result of greater or less degree of survival of primitive conditions. The author has found differences in the Polish and Russian nations. According to Leuzzi(11) in certain lower mammals (frog, lizard, pigeon and cavy) median sural nerve is absent; it exists only lateral sural.

(*a*) The origin of the median sural nerve from the tibial nerve takes place on an average 3 cm. above the level of the knee-joint (range 0–8 cm.). Cases examined 115. Symmetrical in 27·5–60 %.

(*b*) Thickness. Average 1·5 mm. diameter (range 0·5–2·5 mm.) symmetrical in 33·3 % of the 110 cases examined.

(*c*) Course. 99 cases examined.

In 38·4 % the nerve lies very deep under the deep fascia in the interstitial tissue between the two heads of the gastrocnemius muscle in the proximal two-thirds of the leg; in 40·4 % it lay even on the posterior surface of the soleus muscle. This description does not correspond with the usual description of the nerve, viz. that it runs in the same plane and even in the same fascial space as the vein; but the nerve only accompanies the vein in the superficial fascia below the middle third of the leg. The author has never seen any cutaneous branch arising from the nerve which is below the deep fascia.

(*d*) *Relation to deep fascia of calf.* 110 cases examined. The point where the nerve pierces the deep fascia to become cutaneous corresponds to the lower border of the fleshy part of the gastrocnemius muscle and is on an average about 61·4 % of the distance from knee to heel (range 40·5–97·1 %. Symmetrical in 73·3 % of cases).

(*e*) *Relation to small saphenous vein.* Found to be very variable in the 107 cases examined.

Course on the medial side of the vein in 79·7 % (this being the usual description). In nearly 11·2 % the nerve lies on the lateral side of the vein. In the proximal half or two-thirds of the leg the vein and nerve have no immediate relation to one another as the nerve lies in a much deeper plane;

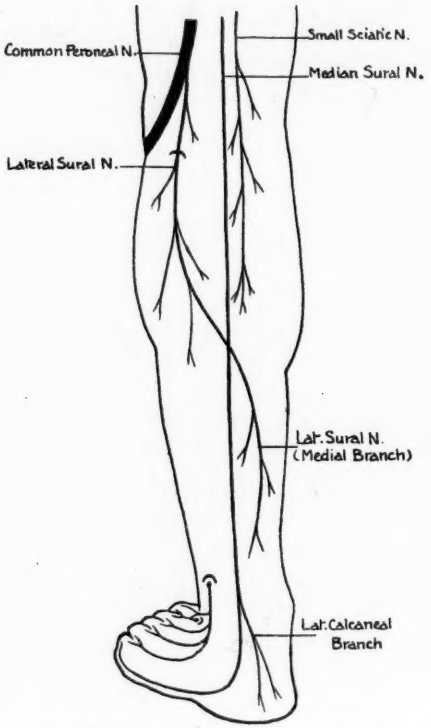

Fig. 1. Type A. 53 %. No communication.

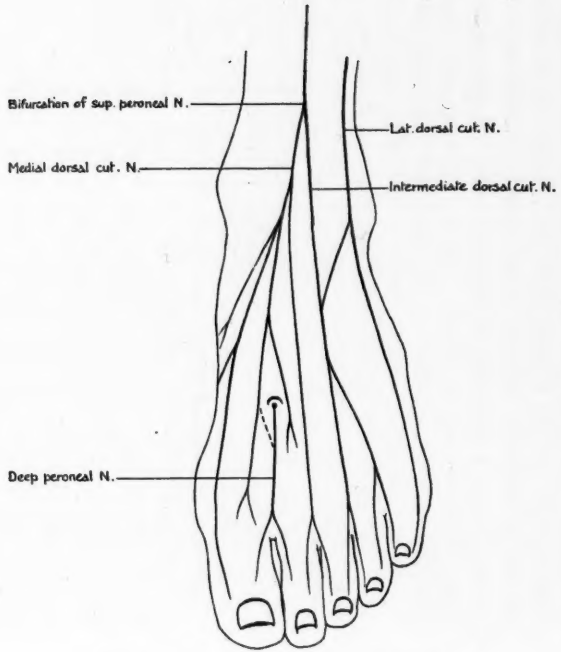

Fig. 2. Type A. Sup. peroneal N. increased.

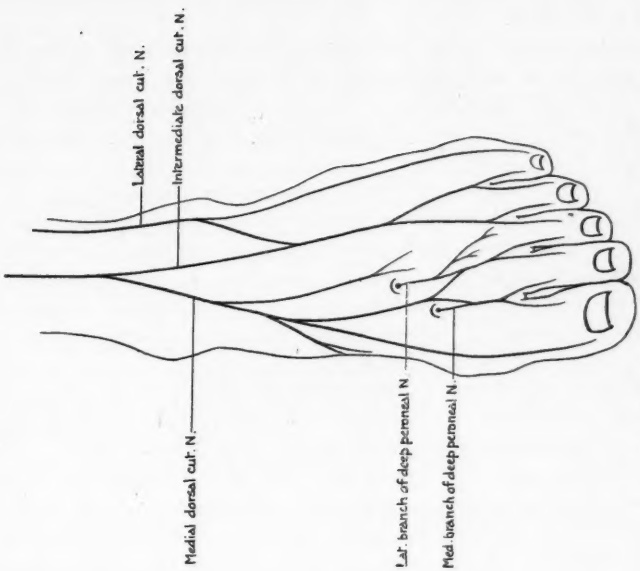
Lateral dorsal cut. N.
Intermediate dorsal cut. N.
Medial dorsal cut. N.
Lat. branch of deep peroneal N.
Med. branch of deep peroneal N.

Fig. 4. Type B. Deep peroneal N. increased.

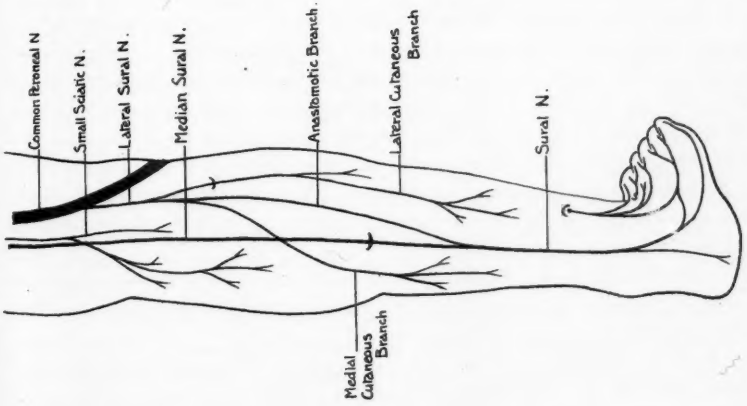

Fig. 3. Type B. 40 %. Formation of Sural nerve.

it is only after the nerve has pierced the deep fascia that it comes into relation with the vein. It is entirely owing to the tortuous course of the vein that the mutual relations of the vein and nerve may be changed several times (2, 3 and even 4).

On an average we can state that in the proximal half of the leg the nerve lies deep and in front of the vein, while in the lower half of the leg it lies at first medial and then lateral to the vein. (Symmetrical in 26·2 %.)

Recapitulation. (i) Variable relations of nerve and veins owing to the variable course of vein.

(ii) Deep situation of nerve in proximal two-thirds of leg.

(*f*) *Terminal distribution of nerve and its relation to the lateral sural nerve.* 118 legs examined. Most important point of present research owing to variations in former descriptions. Research of author results in the distinction of three or even four types of mutual relation of the three main nerves supplying the back of the leg, viz. (i) small sciatic nerve; (ii) median sural nerve; (iii) lateral sural nerve.

Type A (figs. 1 and 2). Main characteristics is the complete lack of communication between the median and lateral sural nerves. This type occurs in 53·8 % cases (according to Catania this type occurs in 35 %, Leuzzi 25 %). The median sural nerve itself descends on the dorsum of the foot as the lateral dorsal cutaneous nerve. The main varieties of this type are evident from the accompanying figures and need no special description. In each case note that the lateral sural nerve approaches the middle line (especially figs. 1 and 3), crosses the middle line superficial to the vein and median sural nerve, and is distributed to the medial aspect of the distal half of the leg. Note also its compensatory relations with the small sciatic nerve, and the lack of cutaneous branches of the median sural nerve in the proximal two-thirds of the leg, the upper part of this area being supplied by branches from the small sciatic nerve and the lower part by the branches from the lateral sural nerve. (L. Bolk met with this arrangement in anthropoids and considers it a transitory stage between the arrangement in lower animals and that in men, in whom we often meet with the union of median and lateral sural nerves to form the single sural nerve.) The medial distribution of the lateral sural nerve reaches on an average as far as 83·9 % of the distance from knee to heel.

The first branches of the median sural nerve are usually lateral cutaneous branches of the heel which arise on an average 82·6 % of distance from knee to heel (range 56·5–96 %).

In B.N.A. terminology this nerve is designated nervus cutaneus surae medialis, but this describes only a few cases and does not agree with (*a*) the deep and exactly median course of the nerve, and (*b*) the complete lack of cutaneous branches in the proximal two-thirds (in many three-fourths) of the leg. The most correct denomination is that used in English literature, viz. medial sural nerve. A modification of the word "medial" to "median"

would be more exact because (*a*) the course of the nerve is really median, and (*b*) it does not give any medial cutaneous branches, these being supplied by the small sciatic nerve in the proximal part of the leg and the lateral sural nerve in the distal part.

Type B (fig. 4). Main characteristic is union beween median sural nerve and anastomotic branches of the lateral sural nerve. Frequency 40·2 % (according to Catania 51 %).

The level of the anastomosis varies as follows: in 10·4 % it occurs in thigh on an average 3·5 cm. above knee-joint (range 2·5–6 cm.); 2·1 % at level of knee-joint; remaining 87·5 % in leg below knee-joint on an average 53 % of the distance from knee to heel (a little below middle of leg, range 5·5–88·9 % below knee, or more exactly (*a*) upper quarter of leg 9·3 %; (*b*) 2nd quarter of leg 18·6 %; (*c*) 3rd quarter of leg 65·1 %; (*d*) lower quarter of leg 7 %). From this whole sum can be subtracted three or four cases where the two nerves were lying closely approximated in the same fascial sheath without actually anastomosing and easily dissected from one another. The length of adherence of the nerves in many cases varied from 5–10 cm. and was also described by L. Bolk in anthropoids.

Type C (fig. 5). Frequency 6 %. Main characteristics are (according to Catania 14 %) as follows:

(*a*) Absence of anastomosis of lateral and median sural nerves to form the sural nerve.

(*b*) Median sural nerve really becomes cutaneous and ends in the region of the lateral malleolus (i.e. in the distal quarter of the leg).

And (*c*) the main trunk of the lateral sural nerve supplies the area usually supplied by the median sural nerve and descends on the foot as the lateral dorsal cutaneous nerve.

In other words there is an inversion of the type *A*, especially as regards the arrangement shown (see fig. 6). Nearly all the cases were asymmetrical except in one male subject. This arrangement is mentioned without growing percentage, only in Cunningham's text-book (p. 762, 5th ed. 1923).

In two cases of this type (1·7 %) the main trunk of the lateral sural nerve sends a small anastomotic branch to unite with the median sural nerve just below the middle of the leg and thus forms a real sural nerve, which however ends in the distal quarter of the leg just above the heel (fig. 18, 4th variety of type *C*).

Type D (fig. 7). Frequency 1·7 % (two cases, not hitherto described). Main characteristics: (*a*) complete and symmetrical absence of lateral sural nerve; (*b*) compensatory increase in the area of distribution of the small sciatic nerve; (*c*) median sural nerve descends on the foot.

Note here the many branches, especially lateral, of the small sciatic nerve innervating an area usually supplied by the lateral sural nerve. This arrangement has not hitherto been described.

The complete symmetry of type *D* in one Russian female subject is very interesting.

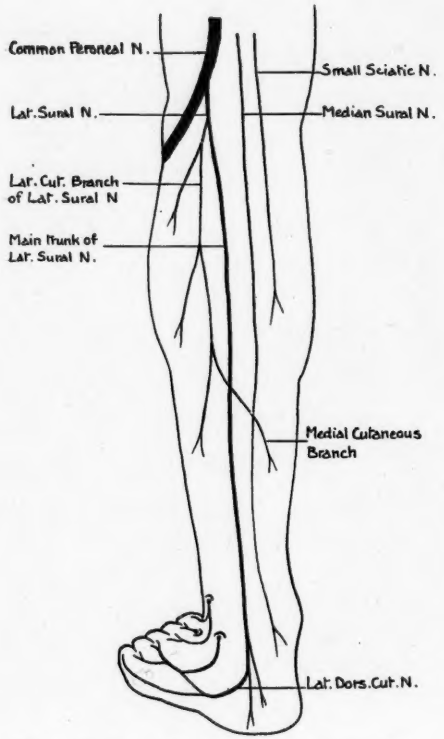
Common Peroneal N.
Small Sciatic N.
Lat. Sural N.
Median Sural N.
Lat. Cut. Branch of Lat. Sural N
Main trunk of Lat. Sural N.
Medial Cutaneous Branch
Lat. Dors. Cut. N.

Fig. 5. Type C. 6 %. No communication. Lat. sural N. becomes lat. dors. cut. N. of foot.

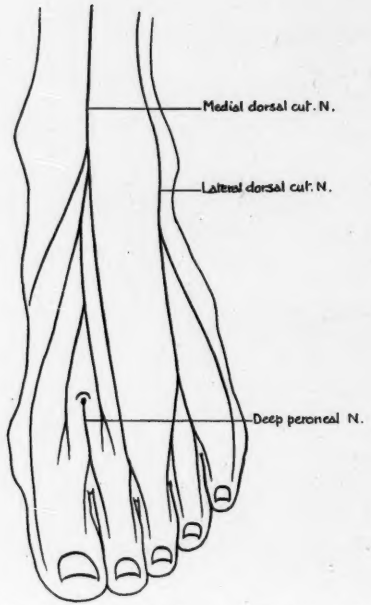

Fig. 6. Type C. Lat. dors. cut. N. increased.

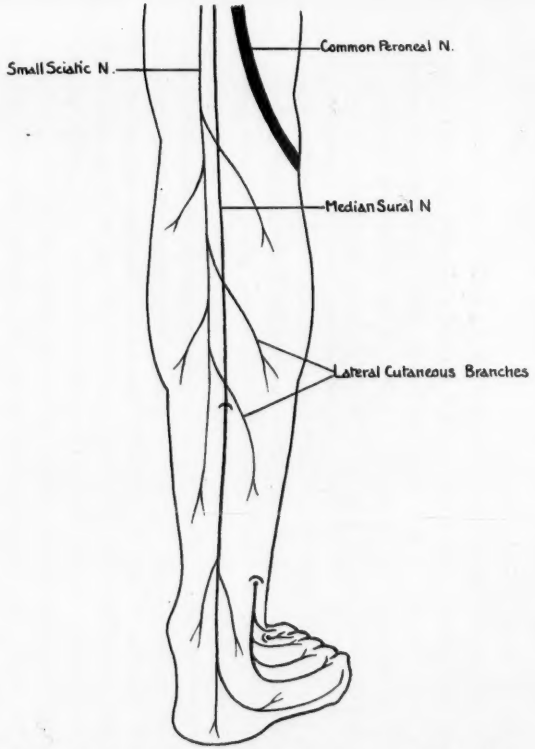

Fig. 7. Type D. 1 %. Lat. sur. N. absent. Small sciatic N. increased. Median sur. N. becomes lat. dors. cut. N.

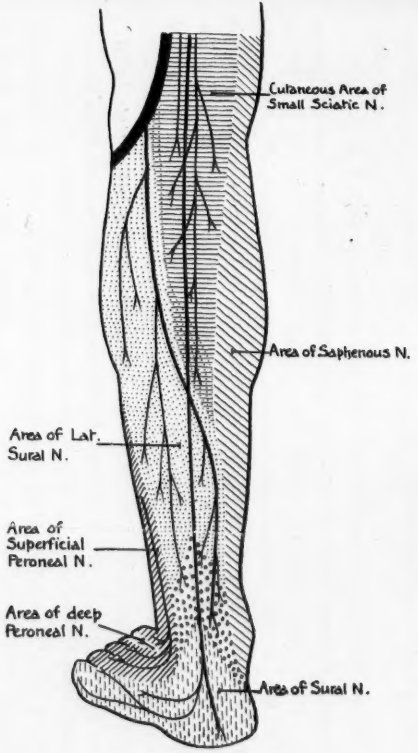
Cutaneous Area of Small Sciatic N.
Area of Saphenous N.
Area of Lat. Sural N.
Area of Superficial Peroneal N.
Area of deep Peroneal N.
Area of Sural N.

Fig. 8.

This arrangement reminds us of the usual state met with in many mammals, viz. some Rodentia, Carnivora, Marsupialae and certain Quadrumana, where we have found the usual absence of the lateral sural nerve, the median sural being well developed only.

3. Lateral Sural Nerve. (N. cut. surae lateralis, B.N.A.)

General characteristics. This nerve arises from the common peroneal nerve about 4·5 cm. above the level of the knee-joint.

In 40·2 % of the cases it sends a communicating branch which unites with the median sural nerve to form the sural nerve. In the remaining cases it is a purely cutaneous nerve of the calf and supplies the lateral side and the distal half of the median and medial aspects of the calf (or, better, medial paramedian).

In 1·7 % (*two cases*) *it is completely absent* (fig. 7) *and that state hitherto has not been described.* This absence is the usual condition met with in many mammals (especially rabbit, cat, dog, sheep).

A. Origin. From the common peroneal nerve on an average (114 cases examined), 4·5 cm. above level of knee-joint. Range 1–10 cm. Only in 30 % was its origin symmetrical (compare the origin of median sural nerves).

B. Thickness. 106 cases examined. Average 2 mm. diameter. Symmetrical in 25 %.

C. Course and relations. 118 cases examined. Very difficult to describe owing to the great variation in course.

After giving a communicating branch to the median sural nerve (in those cases in which it does do so) the lateral sural nerve about the middle (range 35–65 %) of the leg crosses posterior to the small saphenous vein and the more deeply placed median sural nerve, to reach their medial side, and thereafter descends to the medial side of the heel supplying the lower half of the medial surface of the calf. Before crossing the vein the nerve gives off a branch which descends to the region of the lateral malleolus supplying the lower half of the lateral aspect of the calf, the upper half of the lateral aspect being supplied by a special branch from the main trunk given off just below the origin of the lateral sural nerve.

Even in those cases where the main trunk descends on the lateral side of the small saphenous vein (12 %) it nearly always gives off some medial cutaneous branches in the distal half of the leg, which cross superficial to the vein, some of which end in the region of the heel (fig. 5). This distribution of the lateral sural nerve holds good whether or not there is a communicating branch given to the median sural nerve (figs. 1 and 3).

In 9·4 % the lateral sural nerve does not give off any cutaneous branches, in which cases the nerve becomes a real peroneal anastomatic nerve. In all the remaining cases we can confirm (*a*) the lower descent of the lateral sural nerve, and (*b*) the tendency to supply the median and medial aspect of the lower half of the leg.

In 13 % the lateral sural nerve gave off three branches, two cutaneous (medial and lateral) and one anastomatic (which is usually the most medial but sometimes the middle). In 35 % the division into two branches is high, viz. above knee-joint in 15 %, or at knee-joint in 20 %, in remaining 65 % below knee-joint (usually 5–8 cm.).

Only in 40·2 % of cases was an anastomatic branch present, which usually springs from the lateral sural nerve but in two or three cases is given off by the common peroneal trunk.

In 6 % the lateral sural nerve descends to the dorsum of the foot and becomes the lateral dorsal cutaneous nerve, which is usually formed by the median sural or the sural nerve. (In one case the main trunk of the lateral sural nerve became the lateral dorsal cutaneous nerve; in two cases its medial branch and in three cases its lateral branch took on this function) (figs. 12–15).

The lateral cutaneous nerve was absent in two symmetrical cases (1·7 %) and its place taken by the small sciatic nerve.

As the compensatory relations between the small sciatic and lateral sural nerves are important it is useful to summarise the frequency of the extents of the compensation.

(*a*) In superior third of leg	16·9 %	(19 cases)
(*b*) To junction of superior and middle third ...	30	(34 „)
(*c*) In middle third	28·3	(32 „)
(*d*) In lower third	24·8	(28 „)
Total ...	100 %	113 cases

(Nationality and sex have a little influence on the relations of these two nerves.)

D. Fascial relations. 90 cases examined.

Usually pierces deep fascia 38·75 % of distance from knee to heel. Otherwise at junction of superior and middle thirds of leg. Symmetry in 35 %. (Range 1–16 cm. of differences.)

4. Sural Nerve. Frequency of formation 40·2 % (for population of Wilno).

General characteristics. This nerve is a new structure, practically unknown in other animals, even anthropoids.

It is absent in those cases where the median (53·8 %) or lateral (6 %) sural nerve descends to the dorsum of the foot.

It is formed by the union of the median sural nerve and the anastomatic branch of the lateral sural.

Its first important branch is usually (with rare exceptions) the lateral cutaneous nerve of the heel.

A. Origin (or level of junction of anastomatic branch of lateral sural nerve with median sural nerve). Average 53 % of distance from knee to heel (range 0·88 %) or more exactly:

(*a*) Above knee-joint, range 2–6 cm. average 4·5 cm in 10·65 % (5 cases).

(*b*) At level of knee-joint 4·3 % (2 cases).

(*c*) Upper one-third of leg 10·65 % (5 cases).

(*d*) Middle one-third of leg 46·7 % (22 cases).

(*e*) Lower one-third of leg 27·7 % (13 cases).

(Commonest place is just below centre of leg) (figs. 7, 10).

(*a*) Symmetry of level of origin in 21·1 %.

(*b*) Symmetry of absence of union of nerves forming sural nerve 42·2 %.

(*c*) Asymmetry, i.e. absence of union on one side and formation of sural nerve on other 36·7 %.

B. Thickness. Average 2 mm. range 1·25–2·75 mm. diameter. (Symmetry 37·6 %.)

C. Fascial relations. In the majority of cases the nerve descended in the superficial fascia by the side of the small saphenous vein (51·1 %). In the cases of high anastomosis, the upper part of the nerve lies beneath the deep fascia and it pierces the deep fascia to become cutaneous just below the middle of the leg. (Symmetry 22·6 %.)

D. Point of origin of lateral cutaneous nerve of heel. Average 82·6 % of knee-heel distance (i.e. middle of lower fourth of leg). In the cases where cutaneous branches, arising usually from the lateral sural of small sciatic nerve, are absent, the sural nerve supplies cutaneous twigs to the lower fourth (or even third) of the leg.

E. Proportions of sural nerve formed by the anastomatic branch of the lateral sural and the medial sural nerves—as measured by their diameter.

(*a*) Nearly equal: 8·7 % (4 cases).

(*b*) Median sural: anastomatic branch of lateral sural: 2, 3, 5 even 8 : 1 (39·1 %).

(*c*) Anastomotic branch of lateral sural: median sural: 2 or 3 : 1 in 52·2 % of cases (and therefore most frequently).

(Symmetry in the part taken by each nerve on each side in four subjects only.)

Summary

1. The distribution and relations of the nerves of the metazonal region (posterior surface) of the leg is clearly shown in the table (Fig. 9) on p. 290.

2. From that table we can conclude that the lateral dorsal cutaneous nerve of the foot is the continuation of

(*a*)	the median sural nerve in	53·8 %	(63 cases)
(*b*)	the sural nerve in	40·2	(48 ,,)
(*c*)	the lateral sural nerve in	6	(7 ,,)
	Total	100 %	118 cases

3. The denomination of the N. cutaneus surae medialis of the B.N.A. terminology is to be changed to N. surae medianus in Latin, median sural nerve in English, and nerf saphène mediane in French.

4. The name of the main trunk of the N. cutaneus surae lateralis or N. anastomoticus peroneus of the B.N.A. to be changed to N. surae lateralis in Latin, lateral sural in English and nerf saphène externe in French. As regards its branches the names should be as follows—that of the anastomotic branch should be ramus anastomoticus, surae lateralis or ramus anastomoticus peroneus; other branches should be ramus cutaneus surae lateralis, the medial branch crosses the median line and supplies the medial aspect of the lower half of the calf.

5. The existence of the medial cutaneous branch of the lateral sural nerve is nearly constant (90 %).

6. In 1·7 % (2 cases) the lateral sural nerve was completely absent.

7. In 6·0 % (7 cases) the lateral sural nerve descends to the dorsum of the foot.

8. In accordance with the above described arrangement of the relations and distribution of the nerves becoming cutaneous on the back of the leg, the author suggests the subjoined diagram of the cutaneous innervation of the calf (fig. 18).

PART II

CUTANEOUS NERVES OF DORSUM OF FOOT

The sensory innervation of the dorsum of the foot is divided between the superficial peroneal nerve, the deep peroneal nerve and the lateral dorsal cutaneous nerve.

Superficial Peroneal Nerve

This is the main cutaneous nerve of the foot, its branches being the medial and intermediate dorsal cutaneous nerves which supply the greater part of the dorsum of the foot, the deep peroneal and lateral dorsal cutaneous nerves being limited to a small area as a rule.

The variations in the distribution of the cutaneous nerves of the dorsum of the foot are so great that it is possible to distinguish only certain "types" of distribution of individual nerves. Catania (3) has recently given a very complicated description of the types of distribution which is not of much practical value owing to the great number of varieties of distribution depending on the presence or absence of various interconnections between the nerves which he describes. As regards the anastomoses themselves it is important to know the relative sizes of the individual nerves taking part and which have taken the greater part in the innervation of a cutaneous area. If all possible variations of mutual relations of the cutaneous nerves are considered they form nearly 40 different types (see author's diagram). But if we put the anastomotic branches into the varieties of a type we can reduce the number to three main types apart from very rare varieties (based upon the experience of the author).

General characteristics. This nerve usually pierces the deep fascia of the anterior aspect of the leg at the junction of the middle and inferior thirds of the leg as a single trunk and soon afterwards divides into two main

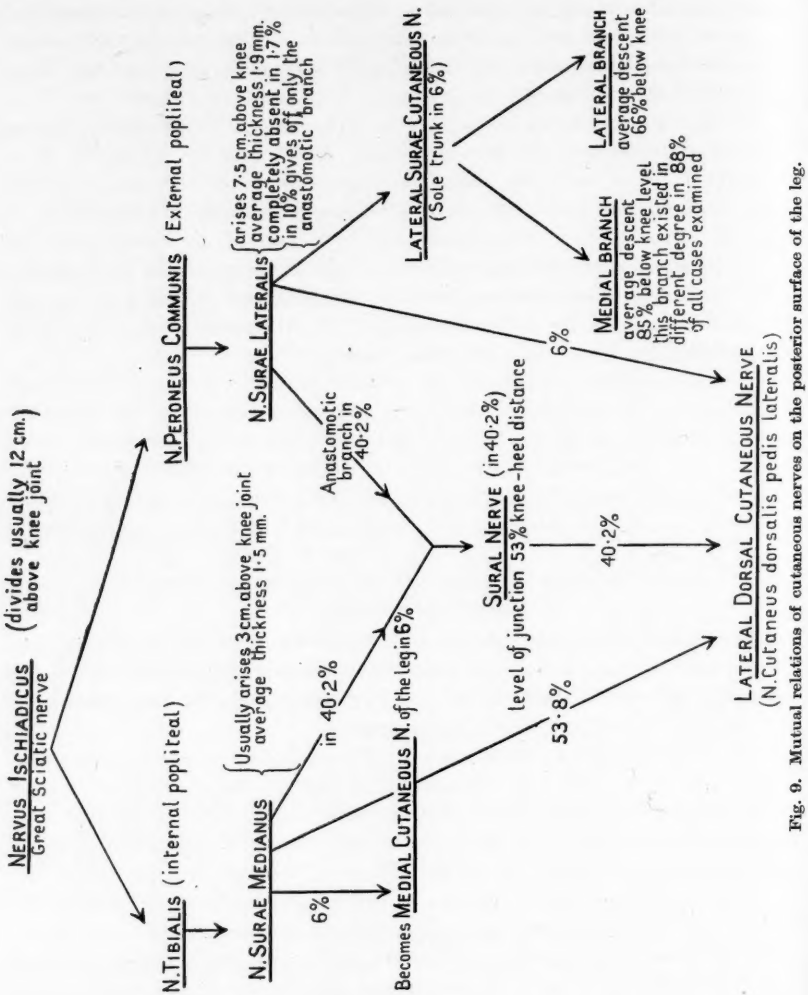

Fig. 9. Mutual relations of cutaneous nerves on the posterior surface of the leg.

branches—the medial and intermediate dorsal cutaneous nerves which descend to innervate the dorsum of the foot and certain toes.

The following conditions were found in the author's researches. In 83 cases

(74·7 %) the nerve divided after piercing the deep fascia, the level of piercing the fascia being 10·5 cm. above the lateral malleolus (or 29 % of the length of the leg). In the remaining 26 cases (23·4 %) the nerve divided higher in the leg before piercing the deep fascia, sometimes dividing as high as a point just below the head of the fibula (Catania reports 20 % of cases dividing high, in all these cases the division being just below the head of the fibula). In such cases both terminal branches of the nerve pierce the deep fascia separately but in each case at different levels, viz.:

(*a*) Medial branch (medial dorsal cutaneous nerve) pierces deep fascia on an average at junction of middle and inferior thirds of left (12·7 cm. or 35 % of length of leg above tip of lateral malleolus; range 18–5 %).

(*b*) Lateral branch (intermediate dorsal cutaneous nerve) pierces deep fascia much lower, about 4·7 cm. above tip of lateral malleolus (range 1–7 cm.) (figs. 20. 21).

Complete absence of the terminal cutaneous branches was noted in one (asymmetrical) case only (0·8 %), the main superficial peroneal nerve ending in the peroneus brevis muscle. Such a distribution has hitherto not been described. In this case the missing cutaneous branches of the superficial peroneal nerve were replaced by (*a*) the lateral dorsal cutaneous nerve, (*b*) enlargement of distribution of the deep peroneal nerve, and (*c*) unusually low descent (in man) of the great saphenous nerve, which nerve in anthropoids usually supplies the medial side of the foot and great toe.

In the following description of the cutaneous nerves of the dorsum of the foot, we commence with the most distal nerve (as explained in the introduction), viz. the lateral dorsal cutaneous nerve, and end with the most proximal nerve, the deep peroneal nerve.

As regards the superficial peroneal nerve, whose position is intermediate between the two nerves just mentioned, its medial branch (medial dorsal cutaneous nerve) is more proximal than the lateral branch because the lateral branch is in close metameric and topographical relation to the distal (in the foetus) peroneus longus muscle while the medial branch belongs to the more proximal peroneus brevis muscle (this difference in the two branches is especially evident in the cases of high division of the superficial peroneal nerve).

Lateral Dorsal Cutaneous Nerve

General characteristics. In anthropoids it supplies the lateral side of the little toe but never supplies the contiguous sides of the 4th and 5th toes (it even may receive an anastomotic branch from the lateral branch of the superficial peroneal nerve (2)).

In man it tends to enlarge its field of distribution in a medial direction and supply the area previously innervated by the lateral branch of the superficial peroneal nerve (intermediate dorsal cutaneous nerve) namely:

Fig. 9. Mutual relations of cutaneous nerves on the posterior surface of the leg.

(*a*) Lateral side of little toe, 100 %.

(*b*) It sends an anastomotic branch to join the intermediate dorsal cutaneous nerve to supply in conjunction with it the adjacent sides of 5th and 4th, and 4th and 3rd toes in 59·8 %.

(*c*) Independently of the intermediate dorsal cutaneous nerve it may supply the adjacent of 5th and 4th, and 4th and 3rd toes (or less often only of the 5th and 4th toes) in 13·7 %.

(The author has not observed any influence of the absence of the anastomosis forming the sural nerve in the leg on the distribution of the lateral cutaneous nerve on the dorsum of the foot.)

Conclusion

A. Absolute enlargement of innervation on dorsum of foot, 13·7 % (16 cases):

(*a*) adjacent sides of 5th and 4th toes 2·6 % (3 cases);

(*b*) adjacent sides of 5th and 4th, and 4th and 3rd toes 10·25 % (12 cases);

(*c*) adjacent sides of 5th and 4th, 4th and 3rd toes and 3rd and 2nd toes 0·85 % (1 case) = 13·7 % (16 cases).

B. Relative enlargement (in conjunction with intermediate dorsal cutaneous nerve), 59·8 % (72 cases):

(*a*) adjacent sides of 5th and 4th toes 8·6 % (10 cases);

(*b*) adjacent sides of 5th and 4th, and 4th and 3rd toes 49·5 % (60 cases);

(*c*) adjacent sides of 5th and 4th, 4th and 3rd, and 3rd and 2nd toes 1·7 % (2 cases) = 59·8 % (72 cases).

Altogether absolute and relative enlargement was present in 88 cases (73·5 %); only in 31 cases (26·5 %) was the distribution limited to the lateral side of the 5th toe (symmetry only 31·6 %).

As regards the anastomotic branch sent by the lateral dorsal cutaneous nerve to the intermediate dorsal cutaneous nerve it was bigger in diameter than the latter nerve in 22 cases (41 %). (Only in one case in *Hylobates syndactylus* (Kohlbrügge) did this nerve supply the lateral side of the 4th toe as well as the 5th toe.)

In man, according to the statistics of the Second Annual Report of the Anatomical Society, the lateral dorsal cutaneous nerve had an increased area of distribution in 35 % of cases, viz. in 27 % as far as adjacent sides of 4th and 3rd toes and in 8 % only adjacent sides of 5th and 4th toes. If this Report includes only the absolute enlargements the differences in the author's figures can be referred possibly to racial influences. According to Catania this absolute enlargement of distribution was stated in 29 %.

INTERMEDIATE DORSAL CUTANEOUS NERVE. (118 cases examined)

This nerve usually supplies the lateral part of the dorsum of the foot and the adjacent sides of 3rd and 4th and 5th toes.

Owing to the varying degrees of anastomosis with the lateral dorsal cutaneous nerve we can distinguish the following types of distribution:

(*a*) the above area of distribution is the most frequent, 73·6 %;

(*b*) enlarged area of distribution 12·7 %;

(*c*) diminished area of distribution 2·3 %;

(*d*) complete absence of nerve (place taken by lateral dorsal cutaneous) 8·6 %, an insufficient development 1·7 %.

MEDIAL DORSAL CUTANEOUS NERVE

This nerve usually supplies the medial part and border of the dorsum of the foot, the medial side of the great toe and the adjacent sides of the 2nd and 3rd toes.

Only in six cases did it receive a communicating branch from the intermediate dorsal cutaneous nerve.

It usually sends an anastomotic branch to the cutaneous branch of the deep peroneal nerve in the first interosseous space (51·7 %).

The following types of distribution of the nerve may be distinguished:

(*a*) usual (above) area—direct or partially indirect—61·8 % (73 cases);

(*b*) dislocation of area of innervation in lateral or medial direction, direct or partially indirect with the deep peroneal nerve, 11 % (13 cases);

(*c*) diminution of area supplied (mostly to medial side of great toe only), 24·6 % (29 cases);

(*d*) enlargement of area supplied (direct or indirect) in two cases only, 1·7 %.

Complete absence of the nerve due to the complete absence of the cutaneous portion of the superficial peroneal nerve (q.v.) was observed in one case (0·8 %).

Total symmetry, 28·8 % (17 subjects).

The anastomotic branch sent to the deep peroneal nerve was bigger than the cutaneous branch of the deep peroneal nerve in 25 %.

Deep Peroneal Nerve (*or more properly its medial cutaneous terminal division*)

In man this nerve usually supplies the adjacent sides of the great and second toes.

In anthropoids (according to Bolk and others) the distribution of the deep peroneal nerve is as follows:

	1md	1lt	2md	2lt	3md.	3lt	4md	4lt
Gorilla 1	.	1	1	1	1	.	.	.
„ 2	.	1	1	1	1	.	.	.
„ of Egsler	.	.	1	1	1	.	.	.
Chimpanzee 1	.	1	1	1	1	.	.	.
„ of Gratiolet ...	.	.	1	1	1	1	1	.
„ of Alex	.	.	1	1	1	1	1	.
„ of Hepburn ...	.	.	1	1	1	1	.	.
Orang-Outang of Westling ...	Complete absence							
„ of Hepburn ...	„							
Hylobates syndactylus	.	1	1	1	1	.	.	.
„ *leuciscus* of Kohlbrügge	.	.	1	1	1	.	.	.

From this table we see that in anthropoids its distribution is larger and dislocated in the lateral direction (the central area is the 2nd, 2lt and 3rd toes).

In the Second Annual Report of the Committee of collective investigation of the Anatomical Society of Great Britain and Ireland (*Journ. of Anat. and Phys.* vol. XXVI) we find the following distribution of the deep peroneal nerve in man as in the following table:

	Sides of toes			
Number of cases	1md	1lt	2md	2lt
217	.	1	1	.
4	1	1	1	.
3	.	1	1	1
1	.	1	.	.
1	Complete absence			
Total 226 cases.				

So that according to English statistics 95 % of the cases showed the usual distribution (see diagram, fig. 9).

Compared with the table in anthropoids we note that:

(*a*) *In man* the area supplied is diminished.

(*b*) That area is dislocated in the medial direction.

(*c*) The area is less variable.

In the author's cases the results obtained were somewhat different from the English statistics, especially as regards increased area of distribution, as follows:

(*a*) Increased area of distribution in 17·1 % (English 3·1 %) or 20 cases (1lt, 2md, 2lt, 3md); in one case it even supplied 3lt 4md in common with the intermediate dorsal cutaneous nerve (in this subject the latter nerve was completely absent on the right side).

(*b*) Usual innervation (1lt, 2md) in 82·9 % (96 cases) as follows: direct 44·4 % (51 cases), indirect 30·8 % (36 cases), mixed 7·7 % (9 cases); (the indirect and mixed innervation can be regarded as a tendency to lose the primitive large distribution in anthropoids).

(*c*) In one case the nerve was completely absent.

Table of author's cases (fig. 34)

Number of cases	Sides of toes 1lt	2md	2lt	3md	3lt	4md	4lt
96	1	1	.	.	.	.	.
17	1	1	1	1	.	.	.
2	.	1	1	1	.	.	.
1	1	1	1	1	1	1	.
1				Absent			
117 cases.	Total symmetry 18·8 %.						

The difference between the English and the author's statistics may be regarded as due to racial differences.

The enlargement of its distribution, according to Catania occurs in 5 % of cases.

Usually the cutaneous division of the deep peroneal nerve pierces the deep fascia at the proximal part of the first interosseous space and afterwards divides into the two digital branches of the adjacent sides of the 1st and 2nd toes, but in 9 cases (7·7 %) the nerve divided before piercing the deep fascia (especially in cases of enlarged distribution). The branches pierce the fascia separately and often at different levels (the lateral branch piercing the deep fascia in the proximal part of the second interosseous space to supply the adjacent sides of the 2nd and 3rd toes) (symmetry in 1·7 %).

As regards the anastomotic branch sent by the medial dorsal cutaneous nerve to the cutaneous part of the deep peroneal nerve, the communication was thick in 22·6 % (12 cases), moderately thick in 22·6 % (12 cases), and thin in 54·7 % (29 cases). In one case there were two anastomotic branches, one to each division of the deep peroneal (cutaneous) nerve.

Symmetry of absence of anastomosis ...	34·2 %	(20 subjects)
Symmetry of anastomosis	29·1	(17 ,,)
Total asymmetry	54·3	(30 ,,)

SUMMARY

1. The great saphenous nerve in man never reaches the medial side of the great toe (this is the usual distribution in anthropoids). Only in one case of the complete absence of the cutaneous branches of the superficial peroneal nerve did the saphenous nerve have a lower descent resembling that in anthropoids.

Thus in man we witness the almost complete disappearance of the saphenous nerve from the innervation of the dorsum of the foot.

2. For purposes of simplicity the following three main types of distribution of cutaneous nerves on the dorsum of the foot may be considered:

Type A. 80 cases (67 %), according to *Sec. Engl. Ann. Rep.* in about 50 % (types, see fig. 1) and according to Catania (1 c. in – 56 %). Then Poland, Italy, Great Britain = 67·5, 56·50. In this type the enlargement of distribution

of superficial peroneal nerve is peculiar to the lower organisation of the cutaneous innervation.

Formula: Md–Prf (Prf–Md_1) Md_1–Md_2 (Md_2–Md_2) Md_2–Lt[1].

The pure type without anastomosis, is only met with in five cases (4·3 %). The remaining 76 cases being mixed cases, the anastomosis being between the deep peroneal and medial dorsal cutaneous nerves or the intermediate or lateral dorsal cutaneous nerves or both together.

Enlargement of distribution of Md_2—11 cases (9·4 %).

Enlargement of distribution of Md_1—1 case (0·85 %).

Enlargement (relative) of Lt—72 cases (59·8 %).

Type B. 20 cases (17·1 %), according to *Engl. stat.* about 3·1 %, according to V. Catania – 6 % (see figs. 35–36).

Then Poland, Italy, Great Britain = 17·1, 6, 3·1.

Formula: Md_1–Prf (Prf–Prf) Prf–Md_2 (Md_2–Md_2) Md_2–Lt.

General characteristic is enlargement of deep peroneal nerve as in anthropoids.

Absolute enlargement Prf 13 cases (11·1 %).

Relative enlargement Prf with Md_1 7 cases (6·0 %).

Type C. 16 cases (13·7 %), according to *Engl. stat.* 36 %, according to ital. statistic of V. Catania (– 29 %, see figs. 35, 36). Then Poland, Italy, Great Britain = 13·7, 29, 36. Characteristic. The enlargement of lat. dors. cut. n. peculiar to man only not present in another mammal. In this type there are three varieties (see figs. 24, 25, 26).

1. Formula: Md_1–Prf (Prf–Md_1) Md_1 (Md_2 (Md_2–Lt) Lt-Lt).

3 cases (2·6 %) of absolute enlargement Lt.

10 cases (8·6 %) of relative enlargement Lt included in the other types.

2. Formula, further enlargement of Lt.

Md_1–Prf (Prf–Md_1) [or Md_2] Md_1 [or Md_2] lt (Lt–Lt) Lt–Lt.

12 cases (10·25 %) absolute enlargement lt.

60 cases (49·5 %) relative enlargement Lt (including other types).

3. Formula—further enlargement of Lt.

Md_1–Prf (Prf–Lt) Lt–Lt (Lt–Lt) Lt–Lt.

Characterised by absence of intermediate dorsal cutaneous nerve and by much lower descent of small sciatic nerve in the legs.

Only one case (0·85 %).

Relative enlargement of this type included in other types in 2 cases (1·7 %).

From the above it is seen that the absolute and relative enlargement in the distribution of the lateral dorsal cutaneous nerve reaches 73·5 %.

Three other very rare types remain to be considered:

Type D. Diminution of area supplied by deep peroneal nerve 1 case (0·85 %)[2].

[1] Md, Medial dorsal cut. nerve. Prf, Deep peroneal nerve medial branch. Md_2, Intermediale dorsal cut. nerve. Lt, Lateral dorsal cut. n.

[2] Reported in the English statistics and that of Catania also (in one case).

Type E. Complete absence of deep peroneal nerve 1 case (0·85 %), fig. 29[1].

Type F. Complete absence of cutaneous branches of superficial peroneal nerve 1 case (0·85 %), fig. 30.

This complete absence of the cutaneous branches of the superficial peroneal nerve has hitherto not been described; the nerve ended in a peroneus brevis muscle and its cutaneous branches were replaced by enlargement of the lateral dorsal cutaneous nerve, the deep peroneal nerve, and the great saphenous nerve along the medial side of the great toe (this last being the usual distribution of the saphenous nerve in anthropoids).

The large cutaneous distribution of superficial peroneal, and especially that of deep peroneal, the restriction of distribution of lateral dorsal cut. nerve and lower descent of saphenous nerve are peculiar to the lower organisation in the development of cutaneous innervation of dorsum of foot in mammals and in man (as well).

[1] Reported also in one case in English statistic of *Sec. Ann. Rep.*

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ON THE DEVELOPMENT OF THE CORACO-BRANCHIALES AND CUCULLARIS IN *SCYLLIUM CANICULA*

By F. H. EDGEWORTH, M.D.

A description of the development of the branchial musculature in Selachii was given by Dohrn, in 1884. He stated that each branchial muscle-plate becomes flattened antero-posteriorly, and finally separates into medial and lateral portions except at its dorsal and ventral ends. The ventral portion forms the deep portion of the Constrictor superficialis, but "diesen Namen verdienen sie freilich nur *cum grano salis*, denn der Constrictor superficialis sollte nur aus denjenigen Muskeln bestehen, welche von den distalen Portionen der ursprünglichen Muskelnschläuche abstammen. In der That sind diese Muskeln auch vorhanden, aber in der Vetter'schen Monographie falsch gedeutet worden. Er beschreibt sie als einen Theil der M. coraco-arcuales, unter dem Namen M. coraco-branchiales; sie haben aber ursprünglich nichts gemein mit M. coraco-hyoideus, setzen sich vielmehr nur an ihm an, durch eine Fascie vom ihm getrennt." (I am not sure of the meaning of the above, so quote it in the original.) No further statement was made, nor were any figures of the Coraco-branchiales published.

In a paper published in 1911 I said, after quoting van Wijhe's statements, that the Coraco-branchiales of *Scyllium* are developed from the ventral ends of all the branchial muscle-plates, which becoming cut off from the remainder of the plates grow back to the shoulder-girdle. I did not make any reference to Dohrn's paper, of which I was ignorant. Allis (1917) stated that in his opinion Dohrn and I had misinterpreted these muscles in embryos, and that they must be developed either from trunk-myotomes, or, possibly, from some part of the coelomic wall. He favoured the former theory on account of the similarity in their innervation to that of the Coraco-hyoideus and Coraco-mandibularis. Allis did not adduce any observations on the development of these muscles either in disproof of my statements or in support of either of his theories.

The following account is the result of a re-examination of the developmental phenomena in *Scyllium canicula.*

In a 12·5 mm. embryo (figs. 1–3) the first four branchial muscle-plates are developed, but the 5th not yet. They are tubular epithelial structures in the branchial segments. They are continuous below with the cephalic portion of the coelom, and their lumina are continuous with the coelomic cavity.

In a 16 mm. embryo (fig. 4) these tubular structures have broadened into plates, and their lumina have disappeared by approximation of their walls.

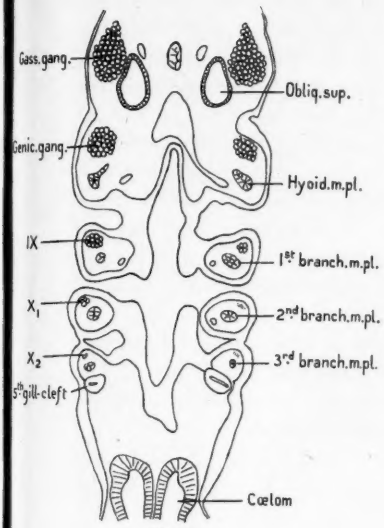

Fig. 1.

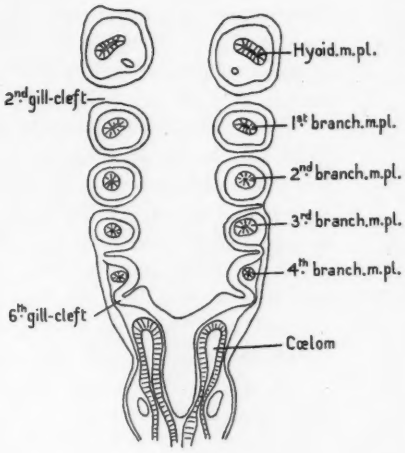

Fig. 2.

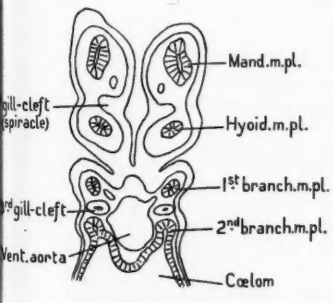

Fig. 3.

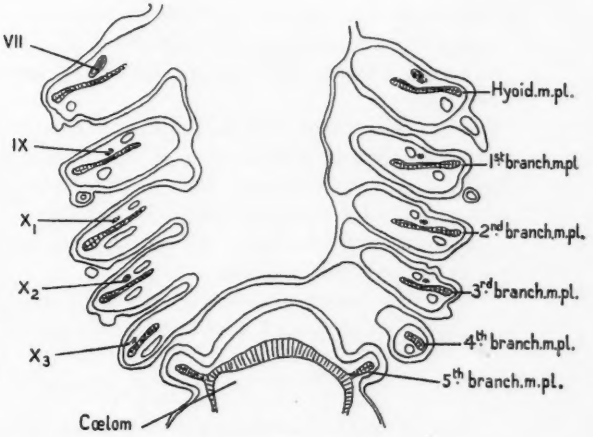

Fig. 4.

Figs. 1–3. Embryo 12·5 mm. horizontal sections. Fig. 2 is ·09 mm. below fig. 1, and fig. 3 ·24 mm. below fig. 2.
Fig. 4. Embryo 16 mm. horizontal section

Each plate consists of two strata of cells, of which the anterior is the thinner. They are directed outwards and backwards at about an angle of 30° from the transverse plane. The plates are broadest at about the middle of the pharynx. Their upper ends are narrow. Their ventral ends are still tubular and join the coelom (fig. 5). The 5th branchial muscle-plate is now developed as a short vertical column of cells which projects as an antero-lateral ridge from the coelom into the 5th branchial arch.

The Coraco-branchiales are developed from the ventral ends of the branchial muscle-plates in embryos of lengths from 23 to 28 mm. They are not formed simultaneously. There is a slight retardation in development, from before backwards, so that in any one embryo various stages of development can be seen in successive segments.

In a 23 mm. embryo (fig. 13) Coraco-branchialis i has already developed and is separated from the remainder of the 1st branchial muscle-plate. The ventral end of the 2nd branchial muscle-plate (fig. 14) is continuous with the coelomic wall. The cells have lost their epithelial character.

In a 25 mm. embryo (figs. 18–20) the 2nd branchial muscle-plate has separated from the coelomic wall. Coraco-branchialis ii is in process of development. It is a longitudinal column of cells, the anterior end of which (fig. 19) is continuous with the muscle-plate. The dorsal edge of this anterior end projects a little further forwards, towards the 2nd branchial bar (fig. 18).

Coraco-branchiales iii, iv, and v are developed similarly, but at slightly later stages—the vth not until the 28 mm. stage.

In a 27 mm. embryo, cut horizontally (fig. 21), the first four Coraco-branchiales are visible. They do not extend backwards beyond their segments of origin.

In an embryo of 29 mm. the Coraco-branchiales have begun to extend further backwards. Comparison of figs. 23 and 24 shows that Coraco-branchialis i is spindle-shaped, and extends from the 1st branchial segment backwards as far as the 3rd branchial segment.

In an embryo of 32 mm. all the Coraco-branchiales have extended backwards to the shoulder-girdle.

The above evidence shows that the Coraco-branchiales are developed from the ventral ends of all five branchial muscle-plates.

CUCULLARIS[1]

I stated (1911) that the upper ends of the branchial muscle-plates increase in antero-posterior extent and, fusing together, extend backwards as the Trapezius to the shoulder-girdle.

Allis (1917) rejected this account, though without making any investi-

[1] I employ the name "Cucullaris" in preference to "Trapezius," as the muscle though genetically connected, is not exactly homologous, with the Trapezius of man.

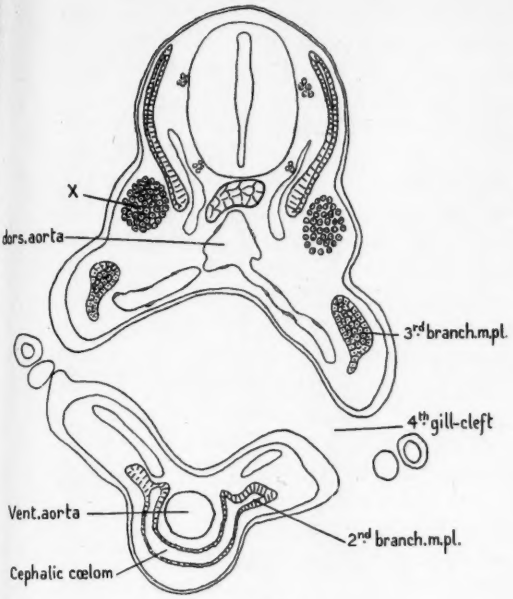

Fig 5.

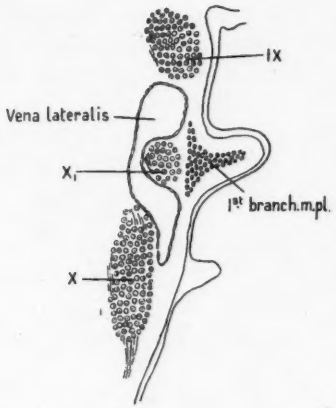

Fig. 6.

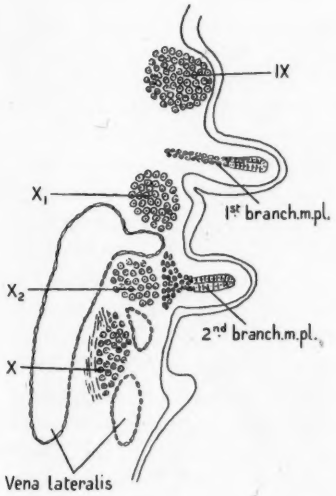

Fig. 7.

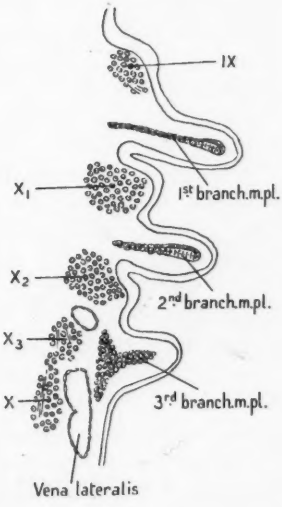

Fig. 8.

Fig. 5. Embryo 16 mm. transverse section.

Figs. 6–9. Embryo 18 mm. horizontal sections. Fig. 7 is ·07 mm. below fig. 6, fig. 8 is ·05 mm. below fig. 7, fig. 9 is ·08 mm. below fig. 8.

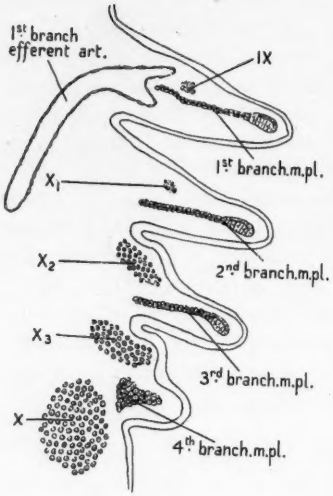

Fig. 9.

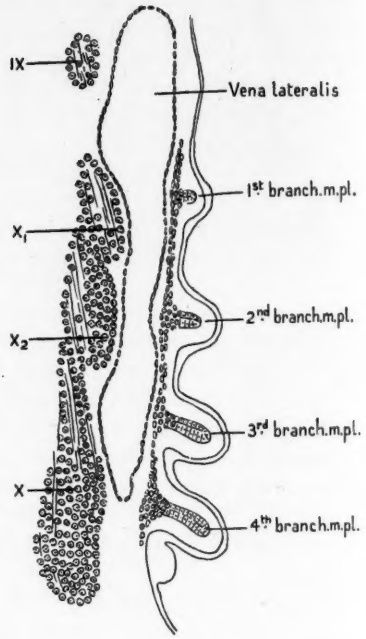

Fig. 10.

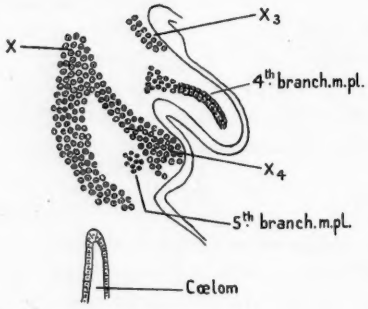

Fig. 11.

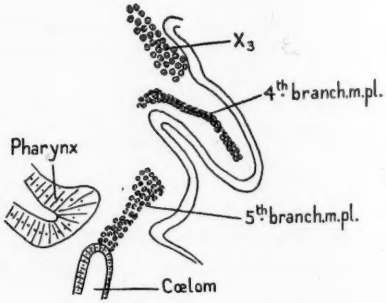

Fig. 12.

Figs. 10–12. Embryo 22·5 mm. horizontal section. Fig. 11 is ·048 mm. below fig. 10, fig. 12 is ·04 mm. below fig. 11.

gations on the development of the musele, and stated that, in his opinion, the muscle is "a differentiation of the ultimate branchial arch," i.e. of the seventh in *Heptanchus* and of the fifth in *Acanthias*, *Scymnus* and *Mustelus*, or "possibly a differentiation of that arch and other more posterior arches if such arches primarily existed and have successively disappeared by reduction or transformation."

In a 12·5 mm. embryo (fig. 1) the upper ends of the branchial muscle-plates are rounded. In one of 18 mm. (figs. 6–9) cells have been proliferated from the inner edges of the upper ends of the first four branchial muscle-plates, forwards and backwards, so that T-shaped structures are visible. That of the 4th is not so fully developed as are those of the first three muscle-plates. The sections figured, like those of the 12·5 mm. embryo, are horizontal ones cut in a plane parallel with the notochord, and on comparison of the figures it is evident that there is a gradually declining height in the muscle-plates, from before backwards.

It may be added that the phenomena figured in the 18 mm. embryo are already present in a 16 mm. embryo, though less pronounced.

In a 22·5 mm. embryo the sections have been cut in a horizontal plane with the posterior end slightly depressed, so that fig. 10 cuts across the upper ends of the first four branchial muscle-plates. It shows that the T-shaped structures at the upper ends of these muscle-plates have coalesced and form a longitudinal column of cells—the primordium of the Cucullaris. The posterior end is just at the junction of the fourth and fifth branchial segments. The greater part of the 5th branchial muscle-plate is still continuous with the coelomic epithelium, but its upper end is free and lies just behind X_4—the branch of the vagus to the 5th branchial segment (figs. 11 and 12).

In a 24·75 mm. embryo (figs. 15–17) the upper end of the 5th branchial muscle-plate has separated from the remainder, and fused with the hinder end of the T-shaped growth of the 4th, which has extended backwards above X_4. The 5th branchial muscle-plate is connected with the coelomic epithelium only at its lower end. The sections were cut in a horizontal plane, so that the anterior part of the Cucullaris is not visible in the sections figured.

In a 28 mm. embryo (fig. 22) the Cucullaris has extended backwards nearly to the shoulder-girdle.

In a 35 mm. embryo a fasciculus diverges from the ventral edge of the muscle in the 4th branchial segment and is inserted into the 5th branchial bar.

The Cucullaris of *Scyllium* is thus developed from cells proliferated from the upper ends of all five branchial muscle-plates.

The above described investigations, which have been carried out on new material, thus confirm the statements I made in 1911 as regards the development both of the Cucullaris and the Coraco-branchiales. They invalidate both the criticisms and the theories of Allis, and show that inferences from adult anatomy are no infallible guide to the development of structures. This can only be ascertained by observation of the actual phenomena.

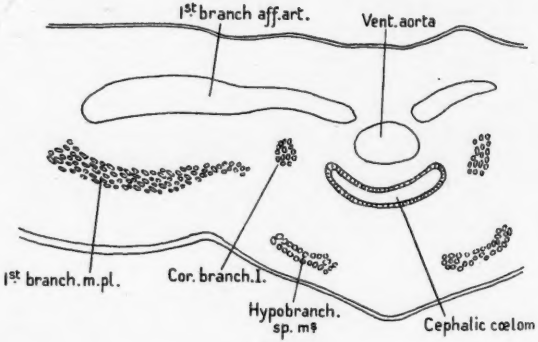

Fig. 13.

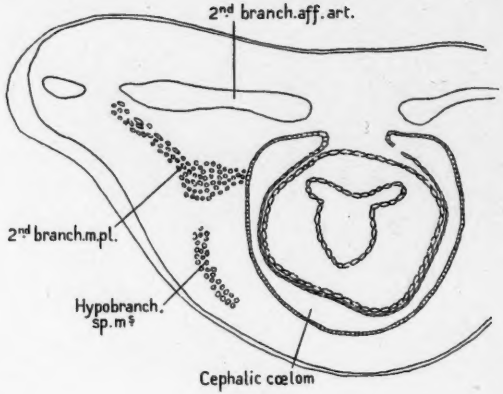

Fig. 14.

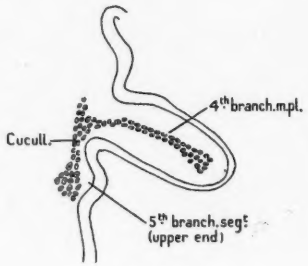

Fig. 15.

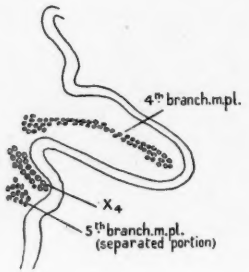

Fig. 16.

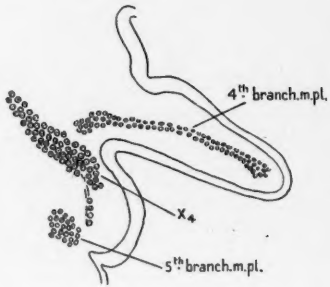

Fig. 17.

Figs. 13, 14. Embryo 23 mm. transverse sections. Fig. 14 is ·18 mm. behind fig. 13.
Figs. 15–17. Embryo 24·75 mm. horizontal sections. Fig. 16 is ·02 mm. below fig. 15, and fig. 17 ·05 mm. below fig. 16.

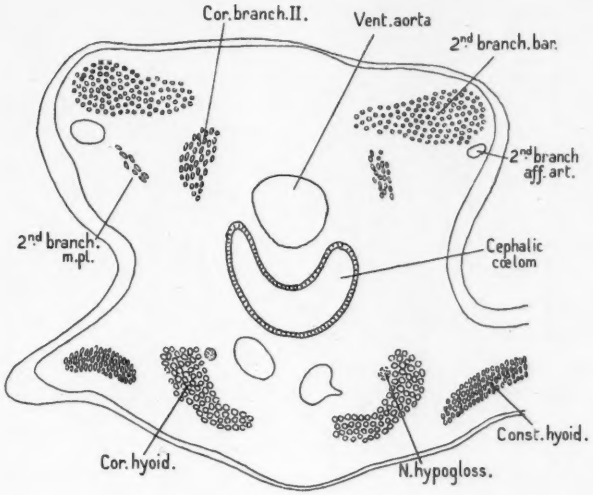

Fig. 18.

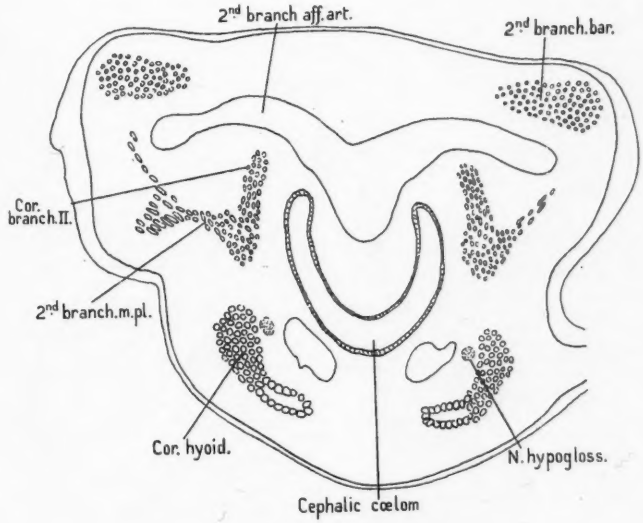

Fig. 19.

Figs. 18–20. Embryo 25 mm. transverse sections. Fig. 19 is ·032 mm. behind fig. 18, and fig. 20 ·04 mm. behind fig. 19. The right side of the sections is a little anterior to the left.

Figs. 15–17. Embryo 24·75 mm. horizontal sections. Fig. 16 is ·02 mm. below fig. 15, and fig. 17 ·05 mm. below fig. 16.

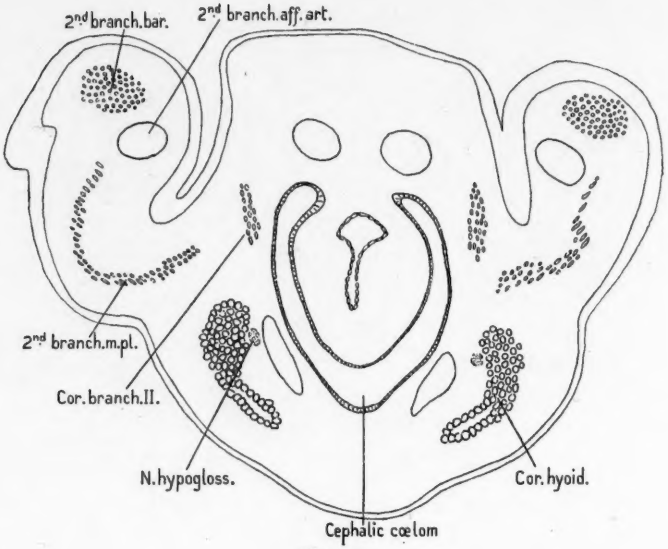

Fig. 20.

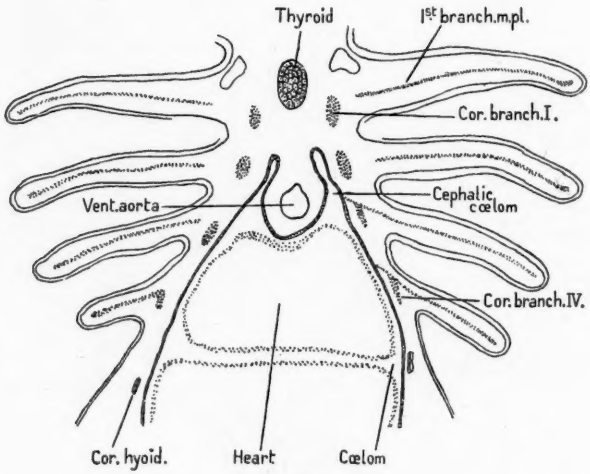

Fig. 21.

Fig. 21. Embryo 27 mm. horizontal section.

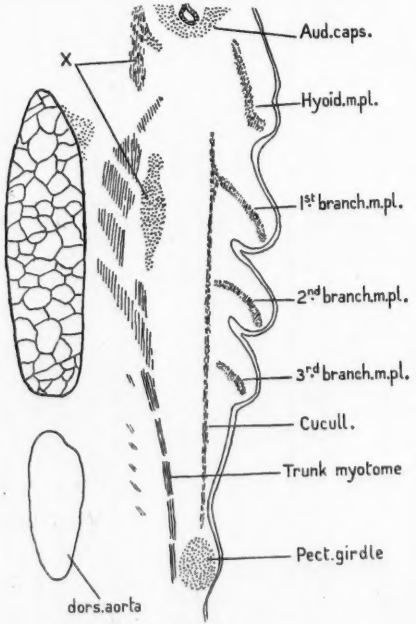

Fig. 22.

Fig. 22. Embryo 28 mm. horizontal section.

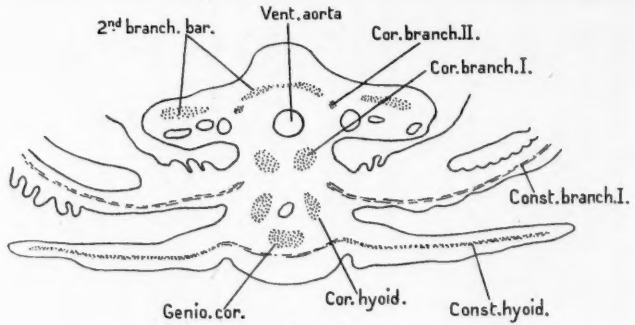

Fig. 23.

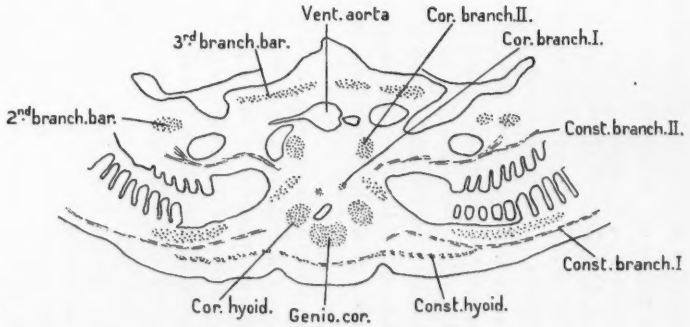

Fig. 24.

Figs. 23, 24. Embryo 29 mm. transverse sections. Fig. 24 is ·12 mm. behind fig. 23.

The development of the Cucullaris is interesting and puzzling. The question arises whether it is the primitive method, or a secondary modification.

In *Scyllium* no Levatores arcuum are developed, but only Constrictores. In *Ceratodus*, as I recently showed, Constrictores are first developed in all five branchial arches, and subsequently Levatores are separated from the inner side of the upper ends of the first four Constrictores. In Teleostomi no Constrictores are developed—but only Levatores.

These facts suggest that, phylogenetically, Constrictores are more ancient than Levatores, and that in this respect Selachii are more primitive than either Dipnoi or Teleostomi.

As regards the Cucullaris—this is developed in *Acipenser* by proliferation from the outer side of the 5th branchial Levator arcus, in *Scyllium* from the upper ends of all the branchial muscle-plates, i.e. of all the primitive Constrictores.

In view of the innervation in both cases from the vagus only—the glossopharyngeus not taking any share—it appears probable that the method of development of the Cucullaris in *Acipenser* is more primitive than in *Scyllium*.

The method of development of the Coraco-branchiales suggests that their innervation by the Plexus cervicalis s. Hypoglossus is a secondary one, and that the primary innervation was by the ixth and xth cranial nerves. In this connection it is interesting to see that there is a Coraco-branchialis v innervated by the xth in *Polyodon*, *Amia*, *Lepidosteus*, *Amiurus*, and *Menidia*, i.e. with a primitive innervation. The causes of such change, if change there has been, are doubtful—possibly by reason of the similarity in function to that of the Genio-coracoideus and Coraco-hyoideus. I hope to discuss this question in a later paper.

The expenses of the investigation and of its publication have been met from a grant of the Bristol University Colston Society.

April 8, 1925.

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ABBREVIATIONS

aff. art., afferent artery; aud. caps., auditory capsule; Cor. branch., Coraco-branchialis; Cor. hyoid., Coraco-hyoideus; Const. hyoid., Constrictor hyoideus; Cucull., Cucullaris; dors. aorta, dorsal aorta; eff. art., efferent artery; Gass. gang., Gasserian ganglion; Genic. gang., Geniculate ganglion; Genio-cor., Genio-coracoideus (Coraco-mandibularis of Vetter); m.pl., muscle-plate; N. hypogloss., Nervus hypoglossus; Obliq. sup., Obliquus superior; pect. girdle, pectoral-girdle; vent. aorta, ventral aorta.

THE NATURE OF MUMMIFICATION AND MACERATION

II. FEMALE AND NEGRO SKULLS

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INTRODUCTION

THE present paper is the completion of a study undertaken to investigate the shrinkage due to drying of the skull before and after maceration. In earlier articles the subject has been fully discussed (1, 2); it will suffice here to give the main results of the investigation on male White skulls; they are the following:

1. A series of forty-nine male White skulls was subjected to mummification and later to maceration, measurements being made weekly.

2. Shrinkage in mummification was found to be complete in eight weeks and equals 0·6 to 0·8 per cent. of the final mummified cranial dimensions.

3. After maceration the cranial dimensions scarcely reached their original value, but, on the average, they came at least to within 0·3 mm. of the green dimensions.

4. After maceration the shrinkage is completed in four weeks and the difference in measurement of the dried macerated cranium from the dimensions of the green skull varies from 0·8 to 1·0 per cent. of the final dried cranial measurements.

5. Mummification, maceration and drying after maceration represent, for practical purposes, merely variations in the water content of the bones. No

unforeseen factors influence the cranial dimensions as a result of these procedures.

6. In its dry state the cranium is sensitive to changes in atmospheric humidity, but the alteration in dimension due to this cause is negligible.

Since these words were penned a new piece of work has been completed upon the comparison of auricular height determinations (3). The skulls for this investigation had had their auricular height determined at varying times about a year previously. For assurance the determination was made once more and to my surprise differences had occurred sometimes approaching, rarely exceeding, 1 mm. Such differences were not to be found in glabellar length. The measurements were made on the Reserve Craniostat (4) and experience shows that the differences were not due to instrumental error. They did not occur in all skulls and there seems to be no other cause for the difference except that of shrinkage affecting the bones directly and hence the relations of face and cranium with consequent slight modification of the cranio-facial axis. It was found that the vertical point had changed in the year 2 mm. on an average in the ten skulls showing alteration out of the fifty-seven skulls in the sample. The statement in paragraph 6 is quite borne out by direct glabellar measurements, but auricular height is complicated by its relationship to the Frankfort plane and a slight fallacy might be induced in the measurement by ignoring this.

It was intended to produce a series of fifty skulls of each sex and of each Stock, White and Negro, but the work has now been in progress four years and for various reasons the female series have not grown so rapidly as was hoped. To wait doggedly for the completion of the tale now seems unjustified and hence it was resolved to finish up the investigation and release time for other researches. We will therefore examine the results upon the material as it stands.

A complicating factor has been the transference of the laboratory to new and more appropriate quarters provided by the generosity of Mr Samuel Mather. Differences between the old and the new buildings in humidity and heating have their bearing in slight measure on the final figures.

THE MALE NEGRO SERIES

Shrinkage in mummification.

The total number of skulls in the male Negro series is forty-eight, but, through an accident, one was cut before measurement and hence the number in Table I (A) is but forty-seven. The method adopted has been exactly the same as for the White males. After stripping off all soft tissues except those in the nose the linear dimensions of the cranium were taken (A). The skull was then cut in the sagittal plane after soaking for twenty-four hours and the brain and membranes removed. A second measurement was made (B) before the skull was allowed to dry. It was measured actually dripping wet. The

drying then commenced in the drying rack at room temperature and weekly measurements were made, the last being at the end of twelve weeks (C). Total shrinkage (D) was ascertained by the addition of shrinkage figures of all skulls in the series, not by subtraction of (C) from (B).

The differences between the means of (A) and (B) show the changes undergone by the skulls as a result of shrinkage in the dissecting room; for practical purposes they are negligible. There is no significant difference in the means even of breadth in spite of the saw cut. This is probably due to the expanding effect of water on the raw edges.

Comparison of the variabilities of (B) and (C) demonstrates that there is no erratic shrinkage in the sample as a whole; hence mummification introduces no unforeseen factor into cranial dimensions.

Table I. *Male Negro crania.*

Mummification.

		Number 47	Mean	S.D.	C. of V.
(A)	Cleaned, moist, not macerated, not cut	Length, S.R.	188·89±0·510	5·19±0·361	2·70±0·188
		Length, glab.	188·51±0·612	6·22±0·433	3·30±0·229
		Breadth	140·60±0·547	5·56±0·387	3·95±0·275
		Aur. height	115·93±0·375	3·82±0·266	3·29±0·229
		Number 48			
(B)	Immediately after section, wet	Length, S.R.	188·83±0·622	6·39±0·440	3·38±0·233
		Length, glab.	188·45±0·605	6·22±0·428	3·50±0·241
		Breadth	140·39±0·533	5·48±0·377	3·90±0·268
		Aur. height	115·84±0·360	3·70±0·255	3·11±0·214
		Number 48			
(C)	Final dry dimensions	Length, S.R.	187·49±0·624	6·41±0·441	3·42±0·235
		Length, glab.	187·06±0·610	6·27±0·432	3·35±0·231
		Breadth	139·58±0·525	5·39±0·371	3·86±0·266
		Aur. height	115·07±0·356	3·66±0·252	3·18±0·219
		Number 48			
(D)	Total shrinkage	Length, S.R.	1·32±0·054	0·554±0·038	41·97±3·351
		Length, glab.	1·41±0·055	0·570±0·039	40·43±3·201
		Breadth	0·83±0·060	0·615±0·042	74·10±7·396
		Aur. height	0·78±0·044	0·448±0·031	57·44±5·730

The sum of the individual differences between the (B) stage and the (C) stage gives the figure set down in (D). It is clear that there is no difference between shrinkage in supra-orbital length and shrinkage in glabellar length. In this the Negro skull differs somewhat from the male White, in which the former dimension shrinks rather more. This difference between the two series is quite natural for there is less difference on the average in the Negro between the two lengths. Breadth shows an extremely erratic variability though not more so than in the Whites, but auricular height is unexpectedly variable; in the White it was much less susceptible to change than any of the other measurements.

Apart from the points commented upon this Negro series behaved in all respects as did the White series.

Total shrinkage on mummification, as before, can be conveniently expressed as a percentage of the final dimension. The figures are:

Supra-orbital length	...	...	0·70 %
Glabellar length ...	...	...	0·75
Euryon breadth	...	...	0·59
Auricular height	...	...	0·68

The only real difference between these figures and those of the male White series is in auricular height. In this measurement the Negro percentage is much less than the White although the variability itself is greater. One must, however, be prepared for differences of these ranges. The only differences which count are those which can be proved statistically and biologically.

Shrinkage after maceration.

After the mummification observations had been completed the skulls were soaked afresh and macerated by the live steam method. While still dripping wet they were again measured and the measurements continued weekly during the drying period until the twelve-week period was complete. Table II

Table II. *Male Negro crania.*

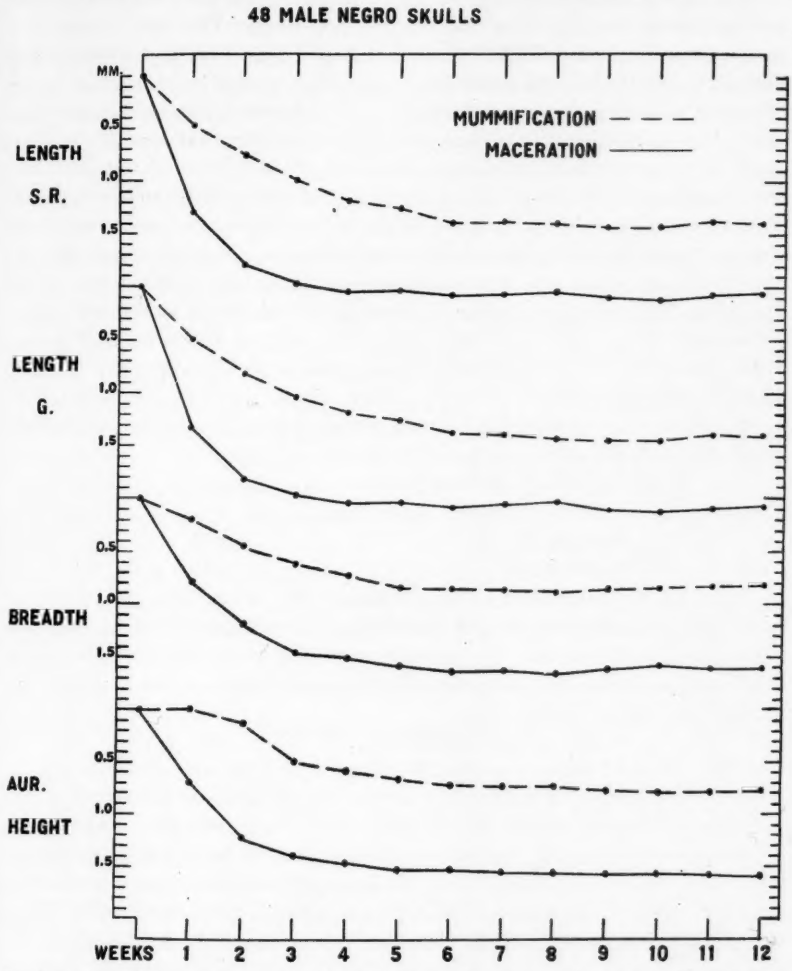
Number 48. Maceration.

			Mean	S.D.	C. of V.
(F)	Macerated, wet	Length, S.R.	188·56±0·612	6·29±0·433	3·33±0·229
		Length, glab.	188·21±0·598	6·14±0·423	3·26±0·224
		Breadth	140·06±0·541	5·56±0·383	3·97±0·273
		Aur. height	115·86±0·361	3·71±0·255	3·20±0·220
(G)	Final dry dimensions	Length, S.R.	186·49±0·621	6·38±0·439	3·42±0·235
		Length, glab.	186·13±0·606	6·23±0·429	3·35±0·231
		Breadth	138·51±0·527	5·41±0·372	3·91±0·269
		Aur. height	114·29±0·357	3·67±0·253	3·21±0·221
(H)	Total shrinkage	Length, S.R.	2·08±0·065	0·673±0·046	32·35±2·227
		Length, glab.	2·06±0·078	0·805±0·055	39·08±3·067
		Breadth	1·55±0·067	0·694±0·048	44·77±3·082
		Aur. height	1·57±0·063	0·645±0·044	41·08±3·280
(I)	Complete shrinkage, i.e. (B) to (G)	Length, S.R.	2·34	—	—
		Length, glab.	2·32	—	—
		Breadth	1·88	—	—
		Aur. height	1·55	—	—

gives the means and variabilities for the dimensions wet (F), the dimensions after twelve weeks' drying (G), the total shrinkage after maceration (H) and the complete shrinkage of the skulls in drying (I), from the moist condition just after section (B) to final drying after maceration (G). It must be understood that the figures for the (H) array are not obtained by subtracting the mean of (G) from the mean of (B), but by the addition of the individual differences.

Comparing Tables I and II it is apparent that, as in the male Whites, there is no significant difference of variability in dimensions whether the crania be measured fresh, mummified, macerated, wet or dry. From this it is apparent that in mummification and in drying after maceration there is

nothing more than dehydration of the bone. There is then no difference in principle between Negro and White skull bone, when judged by this measure.



Graph 1. Graphic representation of shrinkage of linear dimensions in drying male Negro crania. Abscissae indicating shrinkage are at 1/10 mm. intervals. Completion of shrinkage is attained in mummification at the end of eight weeks and after maceration at the end of four weeks. Note the oscillation characteristic of cranial dimensions after shrinkage is completed. This is caused by changes in atmospheric humidity.

Here indeed our work finishes, for it was to inquire into a possible difference in actual bone that this work was undertaken. It is for this reason that we have not continued to enlarge the female series to the size originally con-

templated. There are many minor points, however, which remain before the investigation is properly rounded off and we shall turn at once to these.

Comparing the means of sections (B) and (F) we see that maceration does not restore the skull to quite the original dimensions. The approximation is so close, however, that the difference is negligible. It is perhaps worth noting that, as in the Whites, auricular height is really restored to its original figure, although we shall not find this taking place in the much smaller female series.

In the male Whites we found rather unexpectedly that shrinkage is less after maceration than after mummification. This curious result does not reproduce itself in the Negroes or in the females. One must therefore conclude that its occurrence in the male White series was merely an accident of the sample. The difference in variability of shrinkage in mummification and after maceration are great only in breadth in both male and female Negro series. It appears that these series resemble the male Whites in this feature, shrinkage in breadth being much more orderly after maceration. The very small female White series does not confirm this interpretation, probably simply as a function of the paucity of material.

The percentage in shrinkage on the final dry dimensions after maceration is the following (H on G):

Supra-orbital length	1·11 %
Glabellar length	1·11
Euryon breadth	1·12
Auricular height	1·13

These figures refer solely to the shrinkage after maceration. I have shown that, except in auricular height, maceration does not quite bring back the original green dimensions. By subtracting the means of (F) from the means of (B) we get the following amounts by which the skull, on the average, fails to reach its original dimensions:

Supra-orbital length	0·27 mm.
Glabellar length	0·24
Euryon breadth	0·33
Auricular height	0·02 mm. over-reach.

The figures which we need, however, to give the basis for estimation of the original green dimensions from the final dry dimensions are obtained by subtracting the mean values of section (G) from those of section (B). These are given below together with their percentage upon the final dry dimensions (G):

Supra-orbital length	2·34 mm.	1·26 %
Glabellar length	2·32	1·25
Euryon breadth	1·88	1·30
Auricular height	1·55	1·36

As to the failure of dimensions to reach the original figures after maceration no more than passing notice is required. The amounts are so small as to fall well within the probable error of the mean dimensions. Were it not for

the consistent failure to reach actually the original figures, barring for the moment auricular height, we should not be inclined even to notice them. The amounts of total shrinkage, however, fall into another category. Whether we take the actual figures or the percentages it is apparent that the total amount of shrinkage in this Negro series is about 50 per cent. greater in each dimension than the corresponding figure for the male White series. Further, analysis and comparison of the above tables indicates that no such difference between the two series occurs in mummification; it is only after maceration. The matter may not be dismissed so readily as the other subsidiary problem. We have seen by the comparison of variabilities that there is no difference in principle in the drying of the White and Negro series. These figures now seem to suggest that shrinkage is relatively greater after maceration in the Negro than in the White. From the female series, however, we shall see that this conclusion is not justified, but again is probably simply an accident of this particular lot.

In the sections (D) and (H), Tables I and II of the article on the male White skull(2), by some misunderstanding, a mistake has occurred in setting forth the errors of the mean and standard deviation. These errors were carried to four places of decimals and in the text the significant cipher has been omitted from the first post decimal place. The first line of section (D) should read:

Length, S.R. $1{\cdot}34 \pm {\cdot}0568$ $0{\cdot}590 \pm {\cdot}0402$ $44{\cdot}03 \pm 3{\cdot}540$

I have attempted to avoid the repetition of this error in the present paper by adopting a more uniform arrangement of figures in the tables.

THE FEMALE NEGRO SERIES

Shrinkage in mummification.

The total number of crania in the female Negro series is only eighteen. Alone we should not care to pay much attention to so small a group. Used in relation to the two much larger male series, however, it still may form a useful check upon results and helps materially in the final summary of the work. There is no need to recapitulate statements of method. All sections of Table III are arrived at exactly as in the Negro males and once again section (D) is derived from the individual skulls themselves and not directly from sections (B) and (C).

Changes undergone as a result of shrinkage in the dissecting room are, as expected, negligible (sections A and B). Comparison of the variabilities in sections (B) and (C) shows that there is no erratic shrinkage in the sample as a whole. From section (D) it is plain that no sensible difference exists in shrinkage between supra-orbital and glabellar lengths. Even more erratic variability is present in breadth than in the corresponding males, but with so large an error that the difference is negligible. There are therefore no points

of deviation in the female Negro series from what we have already learned from the two male series.

Total shrinkage on mummification gives the following percentage of the final dry dimensions (D on C):

Supra-orbital length	0·73 %
Glabellar length	0·69
Euryon breadth	0·52
Auricular height	0·81

The differences in these percentages from those in preceding series are not greater than we have learned to accept in our samples. Female Negro mummification results then confirm the male investigation in every way.

Table III. *Female Negro crania.*

Number 18. Mummification.

			Mean	S.D.	C. of V.
(A)	Cleaned, moist, not macerated, not cut	Length, S.R.	181·50±1·118	7·03±0·790	3·87±0·435
		Length, glab.	181·40±1·040	6·54±0·735	3·60±0·405
		Breadth	135·01±0·593	3·73±0·419	2·76±0·310
		Aur. height	110·68±0·493	3·10±0·348	2·80±0·315
(B)	Immediately after section, wet	Length, S.R.	181·49±1·036	6·52±0·733	3·59±0·403
		Length, glab.	181·40±1·028	6·50±0·831	3·58±0·402
		Breadth	135·01±0·585	3·68±0·414	2·73±0·307
		Aur. height	110·66±0·494	3·11±0·349	2·81±0·316
(C)	Final dry dimensions	Length, S.R.	180·18±1·019	6·41±0·720	3·56±0·400
		Length, glab.	180·17±1·021	6·42±0·722	3·56±0·400
		Breadth	134·33±0·517	3·25±0·365	2·42±0·272
		Aur. height	109·82±0·482	3·03±0·341	2·76±0·310
(D)	Total shrinkage	Length, S.R.	1·31±0·063	0·398±0·045	30·38± 4·644
		Length, glab.	1·24±0·063	0·395±0·044	31·85± 3·914
		Breadth	0·70±0·090	0·567±0·064	81·00±13·567
		Aur. height	0·90±0·051	0·324±0·036	36·00± 4·532

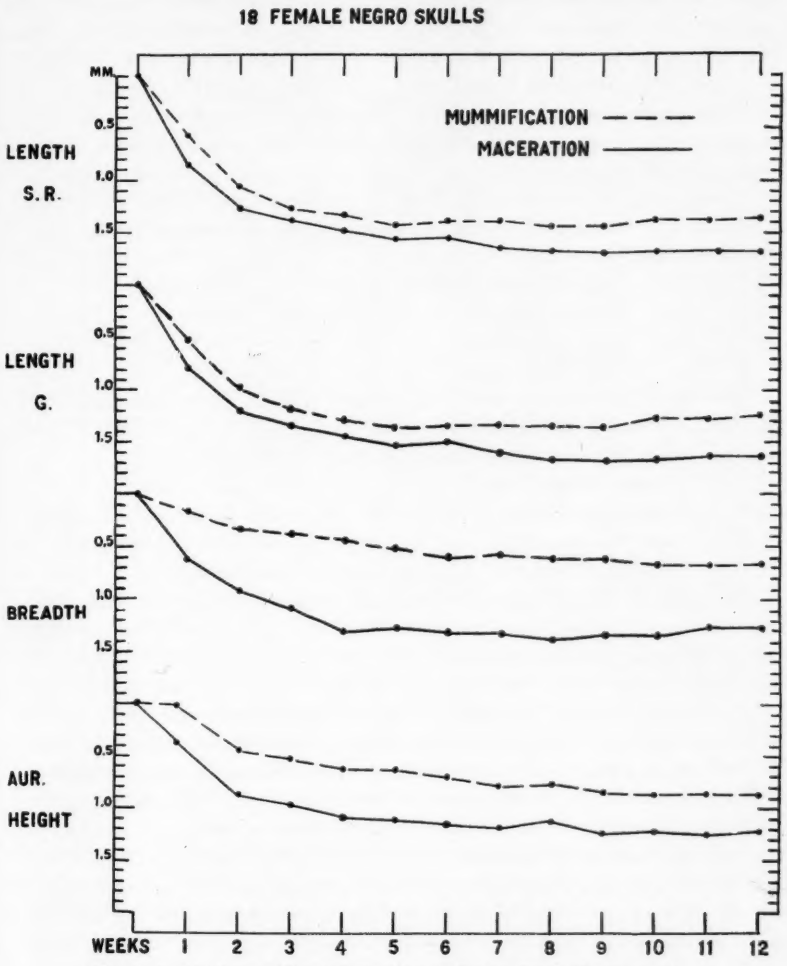
Table IV. *Female Negro crania.*

Number 18. Maceration.

			Mean	S.D.	C. of V.
(F)	Macerated, wet	Length, S.R.	181·22±1·030	6·48±0·728	3·57±0·401
		Length, glab.	181·12±1·027	6·46±0·726	3·57±0·401
		Breadth	134·83±0·544	3·42±0·384	2·54±0·285
		Aur. height	110·54±0·582	3·66±0·411	3·31±0·372
(G)	Final dry dimensions	Length, S.R.	179·46±1·030	6·48±0·728	3·05±0·343
		Length, glab.	179·42±1·030	6·48±0·728	3·05±0·343
		Breadth	133·53±0·547	3·44±0·387	2·56±0·288
		Aur. height	109·32±0·575	3·62±0·407	3·31±0·372
(H)	Total shrinkage	Length, S.R.	1·76±0·098	0·615±0·069	34·94±4·399
		Length, glab.	1·71±0·082	0·515±0·058	30·12±3·690
		Breadth	1·31±0·071	0·445±0·050	33·97±4·239
		Aur. height	1·28±0·094	0·594±0·067	46·41±6·260
(I)	Complete shrinkage, i.e. (B) to (G)	Length, S.R.	2·03	—	—
		Length, glab.	1·98	—	—
		Breadth	1·48	—	—
		Aur. height	1·34	—	—

Shrinkage after maceration.

Once more no significant difference occurs in variability, no matter what the condition of the skulls, except in auricular height and this probably comes



Graph 2. Shrinkage of linear dimensions in drying female Negro crania.

into the category of simple sample accidents (Table IV). There seems to be a somewhat greater uniformity indeed in shrinkage after maceration, but no account should be taken of this feature, which is ruled out by the other series. The most striking fact is the much more orderly shrinkage in breadth after

maceration as testified by the comparison of sections (D) and (H). This has previously been commented upon.

The percentage in shrinkage on the final dry dimensions after maceration is the following (H on G):

Supra-orbital length	0·98 %
Glabellar length	0·95
Euryon breadth	0·98
Auricular height	1·17

These figures, which relate solely to shrinkage after maceration, are intermediate between those of the two male series, less indeed than the Negroes but greater than the Whites.

Subtracting the means of (F) from the means of (B) we find the amounts by which the crania fail to return to their original dimensions by the process of maceration:

Supra-orbital length	0·27 mm.
Glabellar length	0·28
Euryon breadth	0·18
Auricular height	0·12

The figures needed for estimation of the original green dimensions when the final dry macerated dimensions alone are known are given below (B–G), together with their percentage upon the final dry dimensions (G):

Supra-orbital length	2·03 mm.	1·13 %
Glabellar length	1·98	1·10
Euryon breadth	1·48	1·11
Auricular height	1·34	1·23

As in the corresponding male series these figures are greater than for the male Whites, whereas there is no such difference in the mummification results. One might think it simply a matter of drying but, so far as possible, conditions have been kept the same throughout the work. We shall find that the small White female series gives results similar to the Negro series. Now the chief difference existing between the male White series and the other three groups has been the transference from the old to the new laboratory with its improved heating facilities. I am inclined therefore to attribute the evidently greater shrinkage to atmospheric conditions in our new quarters. It is clear that there is appreciable change in linear dimensions of crania following alterations in humidity, although the differences are of so small an order as to be negligible for all ordinary investigations. This subject has already been discussed in the Introduction.

THE FEMALE WHITE SERIES

Shrinkage in mummification.

In this very small series of nine crania it must be remembered that even the large probable errors do not give a fair idea of the variability, but so far as it goes it is useful in conjunction with the three other series previously

considered. The results are given in Table V. As usual there is no appreciable difference in the dissecting room figures and those after soaking and bisection (A and B) and the variabilities in sections (B) and (C) indicate no erratic character of shrinkage. The somewhat greater variability in shrinkage of glabellar length over supra-orbital length (section D) is certainly accidental, for it does not take place after maceration. The variability in shrinkage in breadth is surprisingly small but, in this sample, of no consequence.

Table V. *Female White crania.*

Number 9. Mummification.

			Mean	S.D.	C. of V.
(A)	Cleaned, moist, not macerated, not cut	Length, S.R.	178·16±1·209	5·38±0·855	3·02±0·480
		Length, glab.	177·64±1·248	5·55±0·882	3·12±0·496
		Breadth	139·16±1·304	5·80±0·922	4·17±0·663
		Aur. height	110·58±0·809	3·60±0·572	3·25±0·517
(B)	Immediately after section, wet	Length, S.R.	178·14±1·218	5·42±0·862	3·04±0·483
		Length, glab.	177·77±1·243	5·53±0·879	3·11±0·494
		Breadth	138·94±1·329	5·91±0·939	4·25±0·676
		Aur. height	110·53±0·773	3·44±0·547	3·11±0·494
(C)	Final dry dimensions	Length, S.R.	176·92±1·221	5·43±0·863	3·07±0·488
		Length, glab.	176·75±1·212	5·39±0·857	3·05±0·485
		Breadth	137·77±1·338	5·95±0·946	4·32±0·687
		Aur. height	109·47±0·843	3·75±0·596	3·43±0·545
(D)	Total shrinkage	Length, S.R.	1·22±0·081	0·362±0·057	29·67±5·094
		Length, glab.	1·03±0·087	0·386±0·061	37·48±6·733
		Breadth	1·17±0·075	0·333±0·053	28·46±4·886
		Aur. height	1·17±0·119	0·531±0·084	45·38±7·395

Total shrinkage on mummification gives the following percentage of the dry dimensions (D on C):

Supra-orbital length	0·69 %
Glabellar length	0·58
Euryon breadth	0·85
Auricular height	1·07

For length these are the smallest figures for any of the series, but, small or large, the divergence is not great enough to be of any significance. Comparing all four similar tables, however, we can get an approximate idea of the variability in change of dimensions of small samples during mummification. The suggestion made in my former paper on the male White series, namely, that possibly a relatively small shrinkage in breadth may be associated with non-union of the squamous suture, finds no confirmation here in any of the present three series. Even to make the suggestion was merely the subconscious effect of tradition, a ghost most difficult to lay. In my first paper on this subject (1) I showed to my own satisfaction that age and character of sutures have nothing to do with type or amount of shrinkage. Yet as soon as even a small sample seems to controvert this new interpretation the doubt, raised by tradition concerning what appears to be effective evidence, creeps in afresh. It is therefore with particular satisfaction that I am now able to refute that questionable finding in the male White series and reaffirm my original position.

Shrinkage after maceration.

The comparison of Tables V and VI confirms what we can now take a steadfast stand upon, namely, the similarity of the process of shrinkage in mummification and after maceration. Variability in dimensions remains unchanged whatever the physical state of the crania. In other words neither mummification nor maceration changes the actual composition of the bone so far as we can see from this work, except to alter the amount of contained water. But there is another fact which stands out in marked opposition to

Table VI. *Female White crania.*

Number 9. Maceration.

			Mean	S.D.	C. of V.
(F)	Macerated, wet	Length, S.R.	177·86±1·232	5·48±0·871	3·08±0·490
		Length, glab.	177·58±1·205	5·36±0·852	3·02±0·480
		Breadth	138·67±1·342	5·97±0·949	4·30±0·684
		Aur. height	110·39±0·812	3·61±0·574	3·27±0·520
(G)	Final dry dimensions	Length, S.R.	175·89±1·209	5·38±0·855	3·06±0·486
		Length, glab.	175·64±1·200	5·34±0·849	3·04±0·483
		Breadth	136·61±1·315	5·85±0·930	3·55±0·564
		Aur. height	108·83±0·753	3·35±0·532	3·07±0·488
(H)	Total shrinkage	Length, S.R.	1·97±0·111	0·492±0·078	24·97±4·406
		Length, glab.	1·94±0·129	0·575±0·091	29·64±5·089
		Breadth	2·00±0·191	0·850±0·135	42·50±7·905
		Aur. height	1·56±0·165	0·734±0·117	47·05±8·976
(I)	Complete shrinkage, i.e. (B) to (G)	Length, S.R.	2·25	—	—
		Length, glab.	2·13	—	—
		Breadth	2·33	—	—
		Aur. height	1·70	—	—

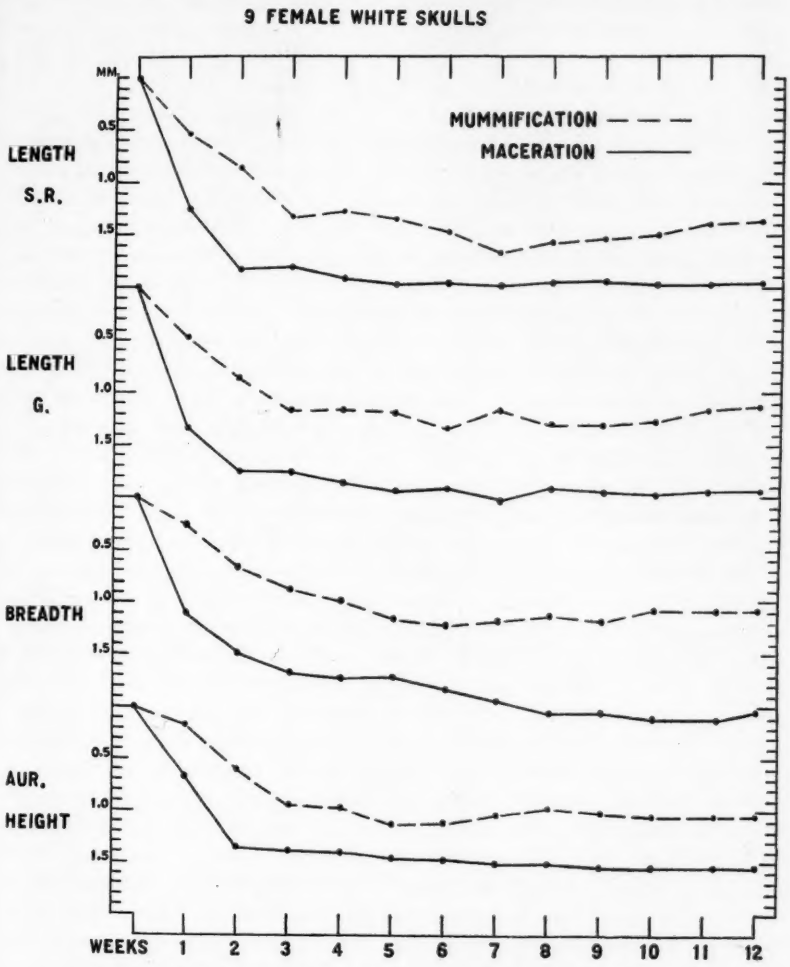
current opinion: the uniform nature of the several variabilities indicates that warping is not a feature of the drying skull. It is true that exhumed crania dried rapidly in the sun do warp, but these are not at all comparable to the series now under examination. If warping occurs in macerated material it is, in my opinion, due entirely to bad maceration. Even a skull in the late teens shows infinitesimal warping when treated by the live steam method. Naturally we are not including the skulls of children in this category: they are an entirely different problem.

More orderly shrinkage in breadth does not occur after maceration in this small series (sections D and H). The phenomenon has previously been touched upon: I believe that there is justification for the conclusion that maceration is ensued by a more orderly and uniform shrinkage in breadth than mummification, for the process of drying takes place more rapidly, and the means of the three larger series are direct evidence upon the point. The small female White group is, I believe, untrustworthy in this feature.

Total shrinkage after maceration can be expressed as a percentage on the final dried means (H on G) in the following figures:

Supra-orbital length	1·12 %
Glabellar length	1·10
Euryon breadth	1·42
Auricular height	1·43

These results confirm the opinion already expressed that total shrinkage is a function of the atmosphere rather than of the character of bone itself.



Graph 3. Shrinkage of linear dimensions in drying female White crania.

Subtracting the means of (F) from the means of (B) we find the amounts by which maceration fails to restore the original green dimensions:

Supra-orbital length	...	...	0·28 mm.
Glabellar length	...	...	0·19
Euryon breadth	...	...	0·27
Auricular height	...	...	0·14

The figures giving the difference in dimension between the fresh green skull and the finally dried macerated skull (B–G) and the percentage of this difference upon the final dried dimensions are the following:

Supra-orbital length	2·25 mm.	1·28 %
Glabellar length	2·13	1·21
Euryon breadth	2·33	1·71
Auricular height	1·70	1·56

In this result, as in all other comparable tables, atmospheric humidity is the prime factor. When we set about to estimate the probable original dimensions of a skull from the known measurements in the dried state we have to cope with this elusive factor. For nearly five years now experiments of this kind have been made in the Reserve laboratory and in the end we are compelled to accept a final result falling far short of the ideal with which we started out. Opinion has shifted with sample after sample: we must be content with a generalisation. Dr Ingalls' experiments on the femur and my own on the cranium, particularly the latter, show considerable range. And it was necessary to assure ourselves that nothing inherent in bone texture or composition is responsible for this range. That now being settled, at least so far as I am concerned, we may concentrate upon the atmospheric factor. But usually this cannot be controlled and hence a survey of the range resulting in an approximate average is the best for which we may hope. Percentages of total shrinkage from the green condition to the dry macerated state lie in this cranial study between 0·81 and 1·71 per cent. with an average of 1·18 per cent. We are now able to express a more definite and final opinion of the shrinkage figure. In my first work (1) I found an approximate average shrinkage of 1·1 per cent. Then Dr Ingalls' studies on the femur, resulting in the lower average of about 0·8 per cent. (5) and my own second study of the cranium with its average of 0·8 to 1·0 per cent. shook my faith in the original larger figure. Now, however, confidence is restored by this final work. The problem involves not simply atmospheric humidity but the subsidiary factor of thickness of bone and consequent ease and speed of water removal. The thicker femur naturally dries more slowly and this is confirmed by the finding that these bones go on shrinking far longer than the cranium before they reach the state of sensitiveness to the condition of the atmosphere. We shall not be far wrong in postulating an approximate average of about 1·0 per cent. for all bones, rather more for the smaller and thinner bones and rather less for the large and thick. For the cranium the average shrinkage is 1·1 to 1·2 per cent. of the final dried macerated dimensions.

COMPARATIVE RATE OF SHRINKAGE: MUMMIFICATION AND MACERATION

Tables VII–XII give the mean amounts of shrinkage in each dimension for every week in the three-month periods of drying. By eight weeks, in mummification, the cranium has reached the stage when oscillation in dimen-

Table VII. *Male Negro crania*

Table VII. *Male Negro crania.*

Mummification. Shrinkage in mm. by weeks of drying.

	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th
Number	47	47	47	47	47	47	48	48	48	48	48	48
Length, S.R.												
Total shrinkage	22·50	13·50	11·25	8·25	2·75	6·75	+0·25	0·50	+1·50	+0·25	+2·00	0·75
Av. shrinkage	0·479	0·287	0·239	0·175	0·058	0·144	+0·005	0·010	+0·031	+0·005	+0·042	0·016
Length, glab.												
Total shrinkage	23·75	14·75	10·25	7·00	3·00	6·00	0·50	+0·75	0·0	0·0	+0·75	0·50
Av. shrinkage	0·505	0·314	0·218	0·149	0·064	0·128	0·010	+0·016	0·0	0·0	+0·016	0·010
Breadth												
Total shrinkage	9·00	12·00	8·00	5·00	5·00	0·50	1·50	0·50	+1·00	+0·50	+0·50	+0·50
Av. shrinkage	0·191	0·255	0·170	0·106	0·106	0·011	0·031	0·010	+0·021	+0·010	+0·010	+0·010
Aur. height												
Total shrinkage	+0·75	11·50	12·50	4·00	3·25	2·75	0·25	0·75	2·25	0·50	0·25	+0·25
Av. shrinkage	+0·016	0·245	0·266	0·085	0·069	0·058	0·005	0·016	0·047	0·010	0·005	+0·005

The figures given are the total and the average amount of shrinkage in mm. for each week of the drying period. Where a plus sign appears there has been no shrinkage during that week but, on the contrary, an increase in dimension. This fluctuation occurs only when the cranium has shrunk to its approximately final dimensions and is measurably sensitive to variations in atmospheric humidity.

Table VIII. *Male Negro crania.*

Number 48. Maceration. Shrinkage in mm. by weeks of drying.

	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	Difference between wet fresh (B) and wet macerated (F)
Length, S.R.													
Total shrinkage	62·25	24·00	8·25	3·00	+0·50	2·50	+0·25	+1·25	2·75	0·50	+2·00	+0·50	−12·25
Av. shrinkage	1·297	0·5	0·172	0·062	+0·010	0·052	+0·005	+0·026	0·057	0·010	+0·042	+0·010	− 0·255
Length, glab.													
Total shrinkage	63·50	24·00	7·50	3·25	+0·25	2·50	+1·25	+1·00	3·25	0·75	+1·25	+1·25	−11·75
Av. shrinkage	1·323	0·5	0·156	0·068	+0·005	0·052	+0·026	+0·021	0·068	0·016	+0·026	+0·026	− 0·245
Breadth													
Total shrinkage	38·00	18·50	13·50	1·50	4·00	2·50	0·0	1·50	+2·00	+1·00	0·50	0·0	−16·00
Av. shrinkage	0·792	0·385	0·281	0·031	0·083	0·052	0·0	0·031	+0·042	+0·021	0·010	0·0	− 0·333
Aur. height													
Total shrinkage	33·75	25·50	8·00	3·25	2·50	0·75	0·75	0·25	0·75	+0·25	0·50	0·0	+ 0·25
Av. shrinkage	0·703	0·531	0·166	0·068	0·052	0·016	0·016	0·005	0·016	+0·005	0·010	0·0	+ 0·005

The figures are the total and average amount of shrinkage in mm. for each week of the drying period. The plus sign is explained in the legend for Table VII. The minus sign in the last column indicates by how much, on the average, the wet macerated cranium fails to reach the measurement of the same dimension in the fresh condition. The plus sign in the same column indicates an over-reach of the original dimension.

Table IX. *Female Negro crania.*

Number 18. Mummification. Shrinkage in mm. by weeks of drying.

	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th
Length, S.R.												
Total shrinkage	10·50	8·75	3·75	1·50	1·00	+0·50	0·0	0·75	0·0	+1·00	0·25	+0·50
Av. shrinkage	0·583	0·486	0·208	0·083	0·055	+0·028	0·0	0·042	0·0	+0·055	0·014	+0·028
Length, glab.												
Total shrinkage	9·50	8·25	3·25	2·00	1·25	+0·50	+0·25	0·75	0·0	+1·50	0·0	+0·50
Av. shrinkage	0·528	0·458	0·181	0·111	0·069	+0·028	+0·014	0·042	0·0	+0·083	0·0	+0·028
Breadth												
Total shrinkage	3·00	3·00	1·00	1·00	1·50	1·50	+0·50	0·50	0·0	1·00	0·0	0·0
Av. shrinkage	0·167	0·167	0·056	0·056	0·083	0·083	+0·028	0·028	0·0	0·056	0·0	0·0
Aur. height												
Total shrinkage	0·25	7·50	1·75	1·75	0·25	1·25	1·50	+0·25	1·25	0·25	0·0	0·25
Av. shrinkage	0·014	0·417	0·097	0·097	0·014	0·069	0·083	+0·014	0·069	0·014	0·0	0·014

Table X. *Female Negro crania.*

Number 18. Maceration. Shrinkage in mm. by weeks of drying.

	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	Difference between wet fresh (B) and wet macerated (F)
Length, S.R.													
Total shrinkage	15·50	7·50	2·00	1·75	1·50	+0·50	1·75	0·50	0·50	+0·25	0·0	0·25	−4·75
Av. shrinkage	0·861	0·417	0·111	0·097	0·083	+0·028	0·097	0·028	0·028	+0·014	0·0	0·014	−0·264
Length, glab.													
Total shrinkage	14·25	7·50	2·25	1·75	1·75	+0·50	1·75	1·00	0·25	+0·25	+0·50	0·25	−5·00
Av. shrinkage	0·792	0·417	0·125	0·097	0·097	+0·028	0·097	0·056	0·014	+0·014	+0·028	0·014	−0·278
Breadth													
Total shrinkage	11·00	5·50	3·00	4·00	+0·50	0·50	0·0	1·50	+1·00	0·0	+1·00	0·0	−3·00
Av. shrinkage	0·611	0·306	0·167	0·222	+0·028	0·028	0·0	0·083	+0·056	0·0	+0·056	0·0	−0·167
Aur. height													
Total shrinkage	6·75	9·25	1·50	2·25	0·25	0·75	0·75	+1·25	2·00	+0·25	0·50	+0·50	−2·25
Av. shrinkage	0·376	0·514	0·083	0·125	0·014	0·042	0·042	+0·069	0·111	+0·014	0·028	+0·028	−0·125

Table XI. *Female White crania.*

Number 9. Mummification. Shrinkage in mm. by weeks of drying.

	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th
Length, S.R.												
Total shrinkage	4·75	3·00	4·25	+0·50	0·50	1·25	+1·75	+0·75	+0·50	+0·25	+1·00	0·0
Av. shrinkage	0·528	0·333	0·472	+0·056	0·056	0·139	+0·194	+0·083	+0·056	+0·028	+0·111	0·0
Length, glab.												
Total shrinkage	4·25	3·50	2·75	0·0	0·25	1·25	+1·50	+1·25	0·0	+0·25	+1·00	+0·25
Av. shrinkage	0·472	0·389	0·306	0·0	0·028	0·139	+0·167	+0·139	0·0	+0·028	+0·111	+0·028
Breadth												
Total shrinkage	2·50	3·50	2·00	1·00	1·50	0·50	+0·25	+0·50	0·50	+1·00	0·0	0·0
Av. shrinkage	0·278	0·389	0·222	0·111	0·167	0·056	+0·028	+0·056	0·056	+0·111	0·0	0·0
Aur. height												
Total shrinkage	1·50	4·00	3·00	0·25	1·50	0·0	+0·75	+0·50	0·25	0·25	0·0	0·0
Av. shrinkage	0·167	0·444	0·333	0·028	0·167	0·0	+0·083	+0·056	0·028	0·028	0·0	0·0

Table XII. *Female White crania.*

Number 9. Maceration. Shrinkage in mm. by weeks of drying.

	1st	2nd	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	Difference between wet fresh (B) and wet macerated (F)
Length, S.R.													
Total shrinkage	11·25	5·25	+0·25	1·00	0·50	+0·25	0·25	+0·25	0·0	0·25	0·0	0·0	−2·50
Av. shrinkage	1·25	0·583	+0·028	0·111	0·056	+0·028	0·028	+0·028	0·0	0·028	0·0	0·0	−0·278
Length, glab.													
Total shrinkage	12·00	4·00	0·0	0·75	0·75	+0·25	1·00	+1·00	0·25	0·25	+0·25	0·0	−1·75
Av. shrinkage	1·333	0·444	0·0	0·083	0·083	+0·028	0·111	+0·111	0·028	0·028	+0·028	0·0	−0·194
Breadth													
Total shrinkage	10·00	3·50	1·50	0·50	0·0	1·00	1·00	1·00	0·0	0·50	0·0	+0·50	−2·50
Av. shrinkage	1·111	0·389	0·167	0·056	0·0	0·111	0·111	0·111	0·0	0·056	0·0	+0·056	−0·278
Aur. height													
Total shrinkage	6·00	6·25	0·25	0·25	0·50	0·0	0·50	0·0	0·25	0·0	0·0	0·0	−1·25
Av. shrinkage	0·667	0·694	0·028	0·028	0·056	0·0	0·056	0·0	0·028	0·0	0·0	0·0	−0·139

sions begins to make its presence felt. This indicates that complete shrinkage has taken place, and thereafter the only change in cranial dimension is produced by sensitivity of bone to atmospheric humidity. A real distinction in the three series represented in these tables, from the male White group previously considered, is the progressive diminution of shrinkage from the very first. There is no tendency to increase the amount of shrinkage during the first three weeks as in the male Whites. Of course we now know that the progressively increasing amount of shrinkage during the first three weeks really means delay in the evaporation of water from the bone. This was characteristic of the old laboratory conditions: in our new building the greatest shrinkage takes place during the first week of drying, as one would expect.

After maceration there is a great shrinkage the first week with marked reduction thereafter and humidity oscillations beginning to make their appearance by the fifth week.

In every important detail the several series now under consideration confirm the results obtained from study of the male White group. The only differences found are due to the better laboratory conditions in our new building. Practically speaking, shrinkage after maceration is complete in four weeks and in mummification the process lasts only eight weeks. Graphs 1, 2, 3 illustrate these facts in more readily appreciable fashion.

MIGRATIONS OF THE EURYON IN DRYING

In its relationship to fluctuation in the site of the Euryon during drying the female White series is uninteresting, for in no one of the nine did the Euryon move either during mummification or after maceration. Both the Negro series, however, exhibit fluctuation. Among the eighteen female Negroes, twelve showed no change in Euryon site during mummification and ten showed no change after maceration. In those crania in which migration of the Euryon took place there was no great movement, merely a swinging of the site between the extreme positions squamous suture and parietal tuberosity, but often not so far. Actually the change in elevation of the bone is infinitesimal and cannot be measured: it is the difference between easy passage and dragging of the Flower's craniometer over the bony surface. There were two female Negro crania in which change of site occurred after maceration but not during mummification, and one which altered during mummification but not after maceration.

Of the forty-eight male Negro crania thirty-one maintained a stable Euryon during mummification and twenty-eight after maceration. Of those in which change occurred thirteen showed migration of the Euryon in one of the procedures but not in the other. In eight migration took place after maceration only: in five it was present in mummification alone.

I have previously shown that age and condition of sutures have nothing to do with migration of the Euryon during drying (1) and there is nought

to add to my previous statement as a result of this survey. It has been possible to show, however, that comparable migrations take place in the position of the vertical point following slight fluctuations in the relation of cranium to face, the result of changes in atmospheric humidity (4). Doubtless these are but two instances of creeping modifications which could be found throughout the bones were there any method of recording them: the nature of bone is itself responsible.

In conclusion I should be altogether lacking in appreciation if I failed to record my obligation to Miss Lindala and Miss Kuenzel, who through many strenuous days have checked the figures and mathematics which form the basic part of this investigation.

SUMMARY

1. This paper is a continuation and conclusion of the work started four years ago to inquire into the physical character of bone. Two articles have previously been published (see p. 328). The present one completes the series.

2. Results are given of shrinkage in mummification and after maceration in three series: forty-eight male Negroes, eighteen female Negroes, and nine female Whites. Measurements have been made weekly.

3. Shrinkage in mummification is complete in eight weeks and, as in the male White group, equals usually between 0·6 and 0·8 per cent. of the final mummified cranial dimensions, although occasionally the shrinkage may approach or even exceed 1·0 per cent. The precise total amount of shrinkage depends upon the condition of the atmosphere. That we find greater percentages in these series than we did in the male White group, and a shrinkage greatest in the first week of drying rather than later, point simply to better drying conditions.

4. After maceration the cranial dimensions scarcely regain their original value, but, on the average, as in the male White, they come at least to within 0·3 mm. of the green dimensions.

5. After maceration shrinkage is complete in four weeks and the difference in measurement of the dried macerated cranium from the dimensions of the green skull, when averaged over the entire four groups of crania, equals between 1·1 and 1·2 per cent. of the final dried cranial measurements. This amount bears out the statement made in my first publication.

6. The amount of shrinkage on drying of any bone is a function of atmospheric condition and size or thickness of the bone itself. It is an index of the ease and rapidity with which water may be withdrawn.

7. Movement of the Euryon during drying is comparable to the recently described movement of the vertical point. It is a phenomenon characteristic of bone which is sensitive to atmospheric humidity. It results from very minute changes in contour of the bone or from modification of the relations of adjacent bones and corresponds to the warping of wood. One must, however, emphasise the fact that there is no actual warping of bone when properly

macerated. Movement of the Euryon is independent of age and of the state of sutural union.

8. Mummification, maceration and drying after maceration represent, for practical purposes, merely variations in the water content of the bones. No unforeseen factors influence the cranial dimensions as a result of these procedures.

9. Although the cranium in its dry state is sensitive to changes in atmospheric humidity, the alteration in dimension due to this cause is negligible in ordinary investigations.

10. No differences in behaviour are recorded as between male and female or between White and Negro.

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A MESODERMAL TUMOUR OF THE TRIGONE OF THE BLADDER IN A FEMALE FOETUS OF THE SIXTH MONTH

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The routine post-mortem of an aborted female foetus of the sixth month led to the discovery of a broadly pedunculated tumour attached to the base of the trigone near the internal urinary meatus. The tumour was roughly pyriform in shape (fig. 1) with the apex distending and occluding the internal

Fig. 1.

urinary meatus and extending along the urethra for a distance of 2 mm. The area of attachment of the tumour lay on a line drawn from the internal urinary meatus to the left ureteric orifice. The wall of the bladder was hypertrophied, but the ureters and kidneys were normal to gross inspection.

On section, the tumour (fig. 2) is seen to be a myxoma. The groundwork consists of a loose network of thin fibres with primitive fibroblasts which tend to be arranged tangentially near the periphery; a few blood vessels are

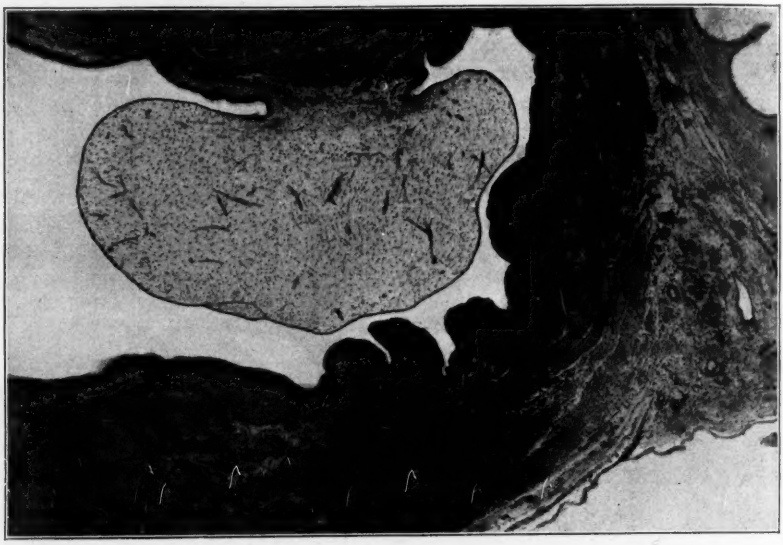

Fig. 2.

present. The normal foetal transitional epithelium of the bladder, three to four cell layers thick, is shown in fig. 3, together with the squamous epithelium consisting of a single layer of cells on the surface of the tumour.

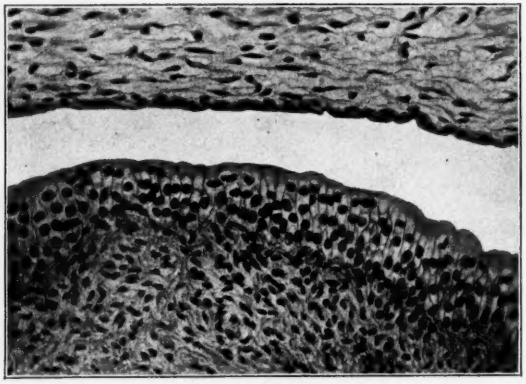

Fig. 3.

The bladder contained about 2 c.c. of foetal urine, and the marked hypertrophy of the musculature of the bladder wall indicates an obstruction to the outflow of urine. This hypertrophy of the bladder wall might be due to the continuous forcible attempts of the bladder to expel the foreign body in the form of the polypus or to the increased work involved in intermittently emptying a full bladder against obstruction.

The Wolffian duct joins the cloaca at the 4·5 mm. stage of the human embryo, and the ureteric-kidney bud appears dorsally on the Wolffian duct near the entrance to the cloaca in the 5·0 mm. stage (fig. 4). The portion of

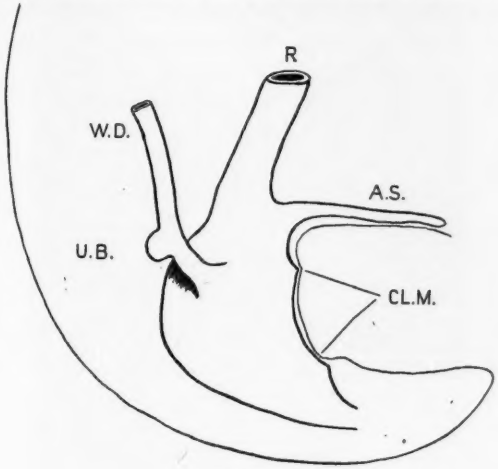

Fig. 4.

the Wolffian duct between the opening of the ureteric-kidney bud and the cloaca is taken up into the urogenital sinus and forms the so-called "cloacal horn." The absorption of this terminal piece of the Wolffian duct into the wall of the bladder gives to the ureter its own direct opening into the bladder as seen in the 11 mm. stage (fig. 5). The portion of the wall between

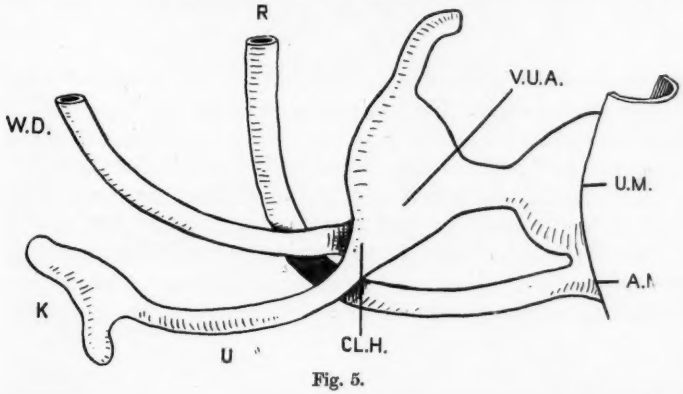

Fig. 5.

the opening of the ureter and the opening of the Wolffian duct begins to grow rapidly so that the opening of the latter remains near the mid-line, whereas the former migrates cranially and laterally. The Wolffian ducts remain close together and they open on a small eminence, called the hillock of Müller, which projects into the lumen of the developing urethra. The triangular area marked out by three points, the Müllerian hillock and the right and left ureteric orifices, is the trigonum vesicae of systematic anatomy and is developed from the expanded lower ends of the Wolffian ducts. The trigonum vesicae is there-

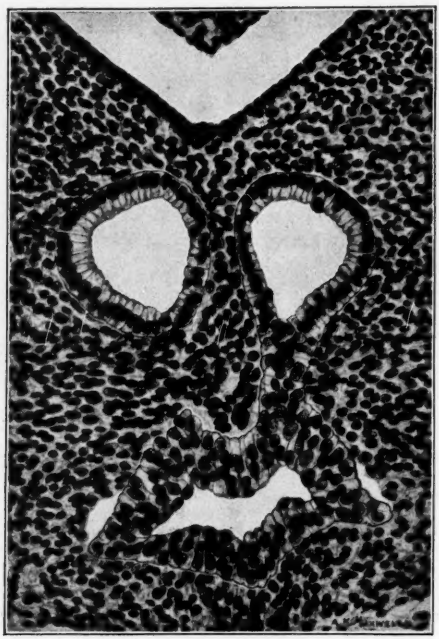

Fig. 6.

fore of mesodermal origin as distinct from the rest of the bladder which is of entodermal cloacal origin. The characteristics of the columnar epithelium of the Wolffian duct as distinct from the transitional epithelium of the bladder are shown in figs. 6 and 7, which are microphotographs from a foetal rabbit of 17·5 mm. In the one section (fig. 6) the Wolffian ducts are shown just before their entry into the prostatic urethra, and in the next section (fig. 7) the Wolffian ducts are shown opening on the Müllerian hillock. The line of demarcation between the two widely different epithelia is clearly shown, and it is suggested that the single-layered squamous epithelium which

covers the tumour (fig. 3) is formed by the stretching out of the columnar epithelium of the Wolffian duct, and not by metaplasia of the many-layered transitional epithelium of the bladder wall. The change from columnar epithelium to squamous epithelium is common in polypi of the nose and cervix uteri, in cysts of the thyroid, and elsewhere. On the other hand, the redifferentiation of a transitional epithelium has not been described.

Tumours of the bladder wall are almost exclusively of the papillomatous and carcinomatous types. Sarcomata of the bladder are rare, and a survey of the recorded cases shows that they are localised entirely to the trigonum vesicae. The limitation of sarcomata to the trigone of the bladder thus confirms that view of the development of the bladder which ascribes to the trigone a

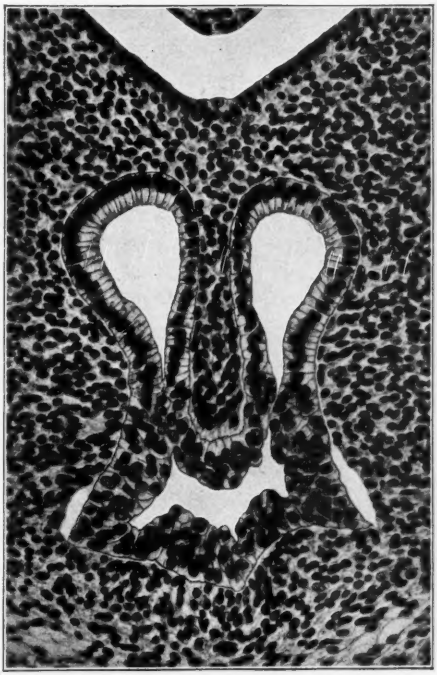

Fig. 7.

purely mesodermal origin from the expanded lower ends of the Wolffian ducts. Thus the foetal bladder under discussion presents a tumour-like malformation due to a defect in tissue—combination between the mesoderm of the Wolffian duct and the entoderm of the primitive cloaca, and may be classified as a dysontogenetic hamartoma. It is interesting to note that

Targett included under the heading of sarcoma all those polypoid growths attached to the lining coat of the bladder in children, which are described as mucous polypi; and to them he ascribes embryonic attributes.

My thanks are due to Professor J. P. Hill, F.R.S., for permission to examine his sections of embryos, and to his technical assistant, Mr Pittock, for the photographs.

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ON THE HOMOLOGIES OF THE PRECHORDAL PORTION OF THE SKULL OF THE HOLOCEPHALI

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The skull of the Holocephali has been frequently more or less fully described, and in all of these descriptions, excepting only my own, the median portion of the actual ventral surface of the prechordal portion of the skull has been considered to be formed, throughout its entire extent, by the trabeculae, the term trabecula being employed to designate the entire trabeculo-polar bar. Under this interpretation of the skull, the septum nasi and the nasal capsules lie on the dorsal surface of the fused trabeculae, and the foramina olfactoria have been so greatly enlarged that the nasal capsules open directly into the anterior end of the cranial cavity without the formation of a posterior bounding-wall. This seemed to me such a marked departure from the conditions found in others of the Elasmobranchii that, in my descriptions of Chimaera (Allis, 1917), I concluded that the fused trabeculae must turn upward at a right angle when they reached the nasal capsules, and, contracted to a narrow rostral stalk which formed the posterior and dorsal edges of the septum nasi, pass dorsal to and between the nasal capsules and then expand into the short beak-like rostrum of these fishes. Attention was however called to the fact that, in Schauinsland's (1903) figure 165, giving a median vertical longitudinal section of an advanced embryo of Callorhynchus, the nasal sac was shown lying definitely dorsal to the so-called trabeculae and definitely in the cranial cavity, at its extreme anterior end; which led one to conclude, as I now see erroneously, that (Allis, 1917, p. 113): "There would accordingly seem to be some error in this figure 165."

Other unusual features in the cranial anatomy of these fishes are: that the orbits of the adults lie dorsal to the forebrain, instead of ventral to it; that there is an unusual number of labial cartilages; that the buccalis lines of latero-sensory organs lie aboral to the nasal apertures, instead of oral to them; and that the efferent mandibular (pseudobranchial) artery of either side lies internal to the palatoquadrate, instead of external to it. The general course of the latter artery was described in my earlier works (Allis, 1912, 1917), but its relations to the palatoquadrate seeming inexplicable, were only briefly alluded to.

These several peculiarities in the cranial anatomy of these fishes may now be considered, and it will be assumed, as in my several recent works, that the polar and trabecular cartilages are, respectively, the pharyngeal elements of

the mandibular and premandibular arches, and that, in connection with the development of the mouth, these two elements swing upward and forward into the plane of the parachordals and the trabeculae then grow forward in the frontal tissues (Allis, 1923*b*, 1925*b*).

A polar cartilage, as a distinct and separate element, has never been described in these fishes. The earliest stages in which the skull has been described are a 60 mm. embryo of Callorhynchus, described by Schauinsland (1903), and a 6 months embryo of Chimaera described by Dean (1906), the former being the younger of the two, for a very considerable portion of its skull is still in the procartilaginous condition. The polar cartilages of this embryo of Callorhynchus are already chondrified, and are indistinguishably fused with each other, with the parachordals, the anterior walls of the otic capsules, the palatoquadrates, and that median portion of the ventral surface of the skull that has heretofore always been considered to represent the trabeculae, and is so designated by Schauinsland. A large plate of cartilage is thus formed, which is perforated at about the middle of its length by three foramina, one median and two lateral, the former of which is traversed by the stalk of the hypophysis, and the two latter by the efferent mandibular arteries, called by Schauinsland the anterior carotids.

The polar cartilages of this embryo of Callorhynchus lie practically at right angles to the parachordals, and they are prolonged, in the same direction, by the prepolar portion of the actual ventral surface of the skull. Because of this, the entire orbito-ethmoidal portion of the skull has the appearance of projecting ventrally, or antero-ventrally, at right angles to its postorbital portion, and the postclinoid wall, which is tall, projects antero-dorsally nearly to the level of the ventral edges of the supraorbital bars. So far as can be judged from the figures given, the hypophysis must have opened on the dorsal surface of the buccal cavity, as it does in the Selachii and Batoidei. The postclinoid wall projects into the plica encephali ventralis, as it does in embryos of the Selachii, and the forebrain has been greatly elongated, and projects ventrally, or antero-ventrally, approximately at right angles to the hindbrain.

In the oldest embryo of Callorhynchus described by Schauinsland the median line of the prechordal portion of the ventral surface of the skull lies in the plane prolonged of the postclinoid portion of the parachordals, and not at right angles to that plane, and this has apparently been brought about by the bending upward and backward of the postclinoid wall, as occurs in certain fishes (Allis = 1923*b*), and not by the bending upward and forward of the polar cartilages. The preclinoid wall is a low rounded ridge that lies immediately beneath the nervi optici.

In Chimaera the conditions are somewhat different from those in Callorhynchus, for a median vertical section of the skull of the adult (Allis, 1917, fig. 2) shows quite definitely that the polar cartilages have been bent upward and forward approximately at a right angle, the bend lying slightly ventral to the point of fusion with the parachordals. From the anterior ends of these carti-

lages the prepolar portion of the median line of the ventral surface of the skull curves gently antero-ventrally at an angle of about 30 degrees to the polar cartilages. There is a large pituitary fossa, the anterior wall of which is formed, as in Callorhynchus, by a low rounded transverse ridge. The foramina for the efferent mandibular arteries perforate the basis cranii slightly posterior to this ridge, and the side walls of the fossa are perforated by the foramina for the pituitary veins. There is no internal carotid foramen, for the posterior portion of the intracranial part of this artery has completely aborted (Allis, 1912). Directly above the preclinoid wall, the cranial cavity is reduced to a narrow passage, or neck, which connects large anterior and posterior portions, the former lodging the forebrain and the latter the mid- and hind-brains. The side walls and roof of this preclinoid neck are formed by the membranous walls of the orbits, these two membranes fusing with each other in the median line, above the neck, to form a large membranous interorbital septum which occupies the entire dorso-anterior portion of the orbits. The nervus opticus perforates the membranous mesial wall of the orbit of its side postero-ventral to this septal portion, at the hind edge of the preclinoid neck and at about the middle of its height.

The walls of that portion of the cranial cavity of the adult Chimaera that lies anterior to the preclinoid neck and lodges the forebrain are wholly of cartilage. The hind edge of its cartilaginous roof lies approximately in the plane of the floor of the postclinoid portion of the entire cranial cavity, and from there the roof slopes gently antero-ventrally to the top of the nasal capsules, its anterior end reaching the external wall of the cranium slightly ventral to the base of the median rostral process. This roof forms the floor of the so-called ethmoidal canal, or more properly chamber, the dorsal portion of this chamber being traversed by the rami ophthalmici superficialis and profundus accompanied by certain blood vessels. The hind wall of the chamber is tall and is formed by the anterior edge of the interorbital septum, which is of cartilage; and the outlines of the chamber, as seen in median vertical longitudinal section (Allis, 1917, fig. 2), strongly suggest that the chamber and the posterior portion of the entire cranial cavity were once continuous, and have been separated from each other by the coming together of the orbits above the forebrain. If this be so, the trabeculae would form the roof of the forebrain chamber, and not its floor, and the early development of these fishes is in favour of this conclusion.

There is, in early embryos of both Callorhynchus and Chimaera, a large knob-like vesicle which lies external to the epiphyseal region, between the midbrain and the forebrain. This frontal-knob is relatively long, but less wide than the forebrain, and Schauinsland (1903) and Dean (1906) differ as to its purpose and function. It is, however, certain that it exerts a downward pressure on the forebrain, and, up to a relatively late stage of development, holds the forebrain and the olfactory nerves and sacs down in their strongly flexed embryonic positions. This prevents the trabeculae (pharyngopremandi-

bulars) from swinging upward and forward into the plane of the parachordals in their usual and normal manner, ventral to the forebrain and concomitant with the reflexing of the brain, and they must therefore, of necessity, pass upward lateral to the forebrain. When they then later grow forward in the frontal tissues they lie dorsal both to the forebrain and the nasal sacs. There they first become connected by membrane (Schauinsland, 1903, p. 81), this membrane later chondrifying to form the roof of the forebrain cavity and the floor of the ethmoidal chamber. The median rostral process of embryos is a direct anterior prolongation of this roof, as it should be, and it and the two lateral processes correspond exactly to the three limbs of the rostral basket of the Carchariidae and Scylliidae, as suggested in my earlier work (Allis, 1917, p. 135).

The trabeculae thus forming the roof of the forebrain cavity, its floor must be formed either by the fusion, in the median line, of the palatoquadrates of opposite sides, or, more probably, by the fusion of those cartilages with tissues that represent the intertrabecular tissues of the Selachii and that were left beneath the forebrain when the trabeculae swung upward lateral to it. The orbits, which are somewhat widely separated in embryos, would, because of the flexed position of the forebrain, come together in the median line above it, and without otherwise changing their topographical relations to the neurocranium would cut the primitive cranial cavity, with doubtless the addition of the cavum praecerebrale, into anterior and posterior portions, the former being the so-called ethmoidal chamber.

The palatoquadrate may now be considered. This element of the skull of fishes is formed either by the epimandibular alone, or by that element of the mandibular arch plus some portions of the epipremandibular, as suggested in my earlier work (Allis, 1923*b*). The primitive dorsal end of the epimandibular is formed by the processus orbitalis and processus basalis together with that portion of the actual dorso-mesial edge of the element that lies between these two processes. The palatine process is either an outgrowth of the epimandibular or, more probably, a part of the epipremandibular. There is usually a more or less developed processus metapterygoideus (muscularis), which is probably an hypertrophied portion of the anterior edge of the groove that primarily extended the full length of the external surface of the element and lodged the blood vessels and nerves of the arch. The efferent mandibular (pseudobranchial) artery always lies postero-mesial to this process, and it primarily lay in the groove between the processus orbitalis and the processus basalis, but in all those fishes in which the lateral dorsal aortae form a circulus cephalicus the efferent artery has been pulled postero-dorsally and crosses the dorso-anterior edge of the pharyngomandibular (polar cartilage). If the pharyngopremandibular (trabecula) were to retain, or reacquire, its primitive attachment to the parachordal instead of fusing with the anterior end of the pharyngomandibular (polar cartilage), the efferent mandibular artery would lie between these two pharyngeal cartilages.

In the 60 mm. embryo of Callorhynchus described by Schauinsland and the six months embryo described by Dean, the earliest embryos of these fishes in which the skull has as yet been described, the palatoquadrate is indistinguishably fused with the neurocranium from its anterior end back to the anterior end of the pituitary fossa, that is, back to the level of the anterior end of the polar cartilage. There the cartilage recedes from the lateral edge of the basis cranii, and a large open space is left which extends posteriorly to the otic capsule, the lateral edge of the opening being formed by a posterior process of the palatoquadrate which fuses with the otic capsule. This opening is called by Dean the palatoquadrate fissure, and it is represented, in the adult Chimaera, by two foramina, the posterior one transmitting the ramus hyomandibularis facialis and the vena jugularis, and the anterior one the ramus palatinus facialis and the arteria carotis externa (Allis, 1917). The efferent mandibular artery runs upward internal to the lateral bounding wall of the palatoquadrate fissure and perforates the basis cranii about half way between the palatoquadrate fissure and the hypophyseal foramen.

In all other fishes the efferent mandibular artery always lies between the processus metapterygoideus and the processus oticus, and never internal to the latter process. The ramus hyomandibularis facialis and the vena jugularis always lie internal to the processus oticus, when that process is present, and hence always internal to the processus metapterygoideus. The ramus palatinus facialis always lies internal to the palatoquadrate, and the arteria carotis externa usually external to that cartilage, one branch of it going to the nasal capsule and another to the ventral surface of the basis cranii.

Comparing these conditions in other fishes with those in the Holocephali, it seems quite certain that the pharyngopremandibulars (trabeculae), in swinging upward and forward lateral to the forebrain have been spread somewhat apart from each other. They have accordingly not been able to fuse with the anterior ends of the pharyngomandibulars (polar cartilages), as they do in other fishes, and have either retained, or reacquired, their primitive connections with the parachordals. The efferent mandibular arteries would therefore lie between them and the polar cartilages, as above explained. This has pushed the artery of either side down along the posterior edge of the epimandibular (palatoquadrate), and it has apparently slipped slightly internal to that edge. It lies internal to the posterior process of the palatoquadrate, that process being therefore a processus metapterygoideus (muscularis) and not a processus oticus, as I formerly concluded. The latter process is not found in any of the Plagiostomi, so far as I know (Allis, 1923*a*), and hence probably not in the Holocephali. The relations of the efferent mandibular artery to the palatoquadrate, apparently so abnormal, are thus readily accounted for.

The labial cartilages are, in all probability, derived from the branchial rays and certain parts of the cartilaginous bars of the premandibular arches. The supramaxillary fold of my descriptions of these fishes (Allis, 1919) would lie approximately external to the line of the trabeculo-polar bars, and its develop-

ment, and the development of that peculiarly protruding portion of the head of the fish that lies ventral to the fold and bears the mouth and nostrils, would be a result of the swinging upward of the trabeculae above the nasal sacs. The position of the nasal apertures ventral to the two lines of latero-sensory organs innervated by the ramus buccalis facialis, would also be thus accounted for, these lines always lying ventral to the nasal apertures in all other fishes. The downward pressure of the frontal-knob, and the related swinging upward of the trabeculae, would cause a displacement and derangement of the mandibular and premandibular myotomes, and the consequent development of muscles from these myotomes that in many respects differ markedly from those in other fishes.

All of the apparently abnormal features of the orbito-ethmoidal portion of the skull of the Holocephali can thus be accounted for if, as I maintain, the polar and trabecular cartilages are, respectively, the pharyngeal elements of the mandibular and premandibular arches, and have swung upward and forward, in connection with the development of the mouth, into a position approximately parallel to the plane of the parachordals. And the fact that this theory offers an explanation of so many features in the cranial anatomy of fishes (Allis, 1924, 1925*a*, 1925*b*, 1925*c*) is added evidence in favour of it.

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A CASE OF MALDEVELOPMENT OF THE RIGHT PAROTID GLAND

By BORIS BOULGAKOW, M.D.
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Cases of maldevelopment of the parotid gland are rare, and this case which was found in an adult male subject in the Anatomy Department is reported as being of some interest.

On dissection of the right side of the face absence of the retromandibular and facial processes of the parotid gland was noticed.

A small portion of gland was found on the anterior border of the masseter muscle in the position where the duct and accessory gland normally turn round the muscle.

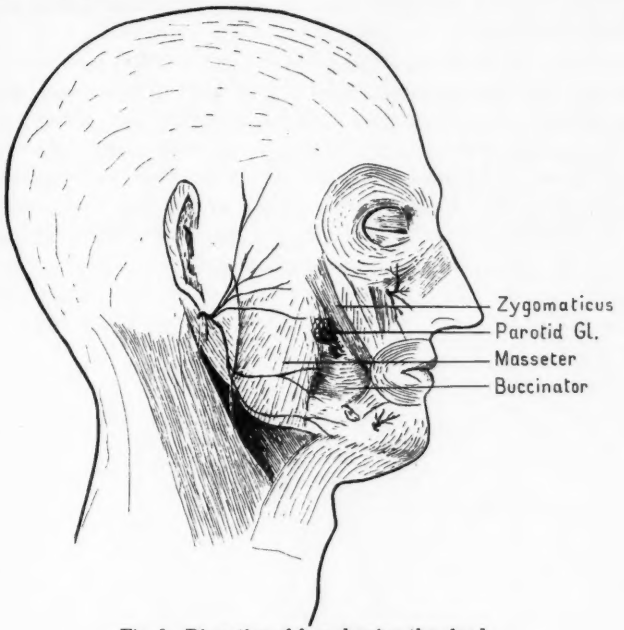

Fig. 1. Dissection of face showing the gland.

The duct was situated normally and opened into the mouth at the line of the second molar tooth.

The facial nerve was found lying free from glandular tissue under the masseteric facia.

The left parotid gland was fully developed as were the other salivary glands.

The lack of other associated abnormalities indicates that the absence of the greater part of the gland is due, not to an early embryonic change, but to arrested development after the gland was laid down.

A CASE OF UNILATERAL DUPLICATION OF THE URETER

By BORIS BOULGAKOW, M.D.,
Curator of Museum, School of Medicine, Cairo
AND DR NASHID FAHMY,
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The abnormality about to be described is not rare and our only apology for publishing it, is that we consider that the more important details of all such cases should be recorded.

The kidney was found in its usual position in the left lumbar region and being covered by its capsule, appeared at first sight to be normal; when however the capsule was removed, a striking difference was observed to exist between the upper and lower parts; the upper third was brighter in colour and more distinctly lobulated than the lower two-thirds. A distinct line of demarcation separated the two areas. Each of the two areas had a hilum of its own. Three arteries entered the kidney (fig. 1) as follows: the highest one

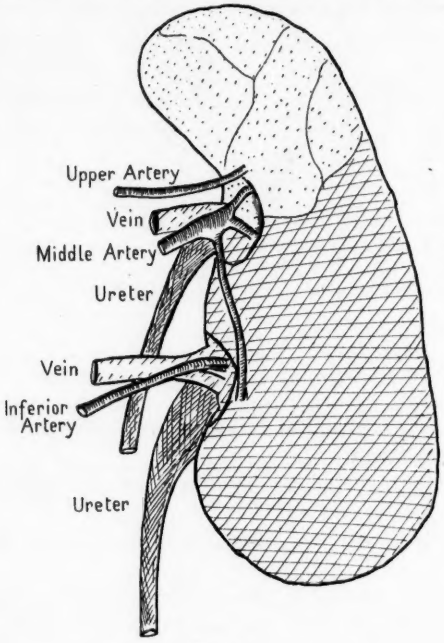

Fig. 1.

appeared as if it might have been a branch of the suprarenal artery, but it was impossible to be certain of this as the kidney had been removed before we saw it. This vessel entered the substance of the upper lobulated part above its hilum. The second artery, a rather big trunk, was directed towards the upper hilum and supplied a branch to the lower hilum. The third one or inferior artery entered the kidney through the lower hilum. Both the middle and inferior vessels were branches of the aorta.

The veins, which were two in number, were situated behind the arteries.

The measurements of the kidneys were as follows:

	Right	Left
Length	10½ cm.	11½ cm.
Breadth	5 „	5½ „
Thickness	3½ „	3¼ „
Weight	148 gr.	155 gr.

When a section of the kidney was made, two separate pelves, surrounded by cortical and medullary layers could be made out. The upper pelvis divided into two main branches, three papillae opening into the calices of these branches. The lower pelvis was larger and divided into three main branches, five papillae opening into the calices of these branches. A separate ureter emerged from each of the pelves and opened separately into the bladder. Their internal orifices were separated by a distance of 4 mm. Before entering the bladder, the two ureters were bound together by connective tissue for a distance of about 1 cm. (fig. 2).

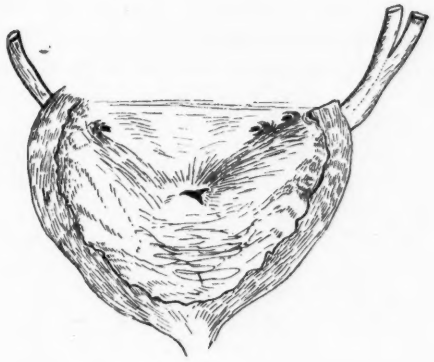

Fig. 2.

A somewhat similar case was recorded by Wakeley in the *Journal of Anatomy and Physiology*, vol. XLIX, 1914–15. In dealing with the causation of the condition, Wakeley discusses the theories of Pohlman and Huntington with regard to the origin of double ureters. He supports Pohlman's theory, i.e. that the condition is probably due to division of the renal bud.

The case we have just recorded might be taken as supplying evidence in favour of either Pohlman or Huntington's theory. If we adopt Pohlman's theory, we can regard the duplication as being brought about by a complete splitting of the renal bud and absorption of that portion of the Wolffian duct between the point where it opens into the cloaca and the point where the renal bud arises. Thus each ureter comes to have a separate opening into the cloaca or at a later stage into the bladder. This explanation is supported by the fact that near their termination in the bladder both ureters were surrounded by connective tissue and formed one mass, which would indicate absorption of that portion of the Wolffian duct between its opening into the cloaca and its junction with the renal bud.

If we adopt Huntington's theory, viz. that the additional ureter is derived from a separate renal bud, then we should have two renal buds growing up towards the Wolffian body, from which is formed the secretory portions of the kidney. Each renal bud gives rise to a ureter with its pelvis and calices. In support of this explanation we have the difference observed between the upper third and the lower two-thirds of the kidney.

In conclusion we suggest that this case may be regarded as an abnormal development of the ureter from the Wolffian duct and that the Wolffian body was normally developed. This latter fact is proved by the presence of a common capsule and common arterial vessels. The difference in colour and the persistence of lobulation in the upper portion of the kidney we regard as being due to incomplete development brought about by the upper ureter reaching the Wolffian body at a later stage than the lower one.

We have to express our thanks to Professor D. Derry for his assistance given us in writing this paper and to Dr McKelvey for his help in correcting it.

THE INNERVATION OF THE HEART

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THE object of this investigation was to determine if possible the distribution of the vagus and sympathetic fibres of the heart.

Recent work has given great importance to the various aspects of the problem of double innervation. An attempt was therefore made to see if a combined morphological and experimental investigation of a doubly innervated organ such as the heart would add to our knowledge of the manner in which such a type of innervation is arranged.

The morphological investigation of the effects of removal by experiment of one of the two innervating systems in an organ like the heart does not seem to have been carried out hitherto. Discussing the whole problem of nerve regeneration Boeke remarks that in the autonomic system the results as yet await investigation.

It was apparent from a study of the literature that such an investigation was beset with peculiar difficulties. In regard to methods Boeke has referred to the results obtained by staining with methylene blue as being extremely capricious, while on the other hand he states that he was only able to demonstrate the intra-protoplasmatic endings of the cardiac nerves by the silver pyridine method when he allowed his material to remain in the fixative for six months. Moreover silver methods have the added difficulty that it is hard to distinguish between connective tissue elements and nerve structures.

Moreover it was apparent that there were large numbers of disputed points to be settled before an experimental morphological study could be securely interpreted. The literature on the innervation of the heart is enormous. We have consulted those papers of the earlier investigators which we thought were the more important. We have used the summaries provided in Mollard's monograph on the nerves of the heart published in 1908 and also in Müller's *Die Lebensnerven* published in 1924. While our work was in progress there appeared two papers on the same subject, one by Fukutake and another by Perman. Both of these contain full references and an abundant discussion of the literature.

I wish to express my thanks to Professor Elliot Smith for the interest he has taken in this work and for the facilities he has afforded me.

METHODS

After many preliminary trials we accepted the verdict of the experience of others and abandoned gold chloride and silver for staining the nerves of the heart. All our material has been stained by the methylene blue method.

This was injected as 0·05 per cent. solution of the dye in normal saline into the aorta and so through the coronary arteries. This was done soon after the death of the animal. After allowing the material to take up the dye for about half-an-hour the material was divided into pieces of small thicknesses and the nerves allowed to "blue up," the process being controlled by observation. The material was afterwards fixed in ammonium molybdate and placed in the ice chest. After washing in running water it is important to fix immediately by carrying it into the highest alcohols. The clearing was done in oil of wintergreen and pieces of any size providing they are not too thick can be cleared in this way. By clearing through benzol into paraffin we have been able to obtain excellent sections, which are best mounted in oil of wintergreen. Xylol and low strengths of alcohol are to be avoided.

The experimental material consisted of cats from which the stellate ganglia were removed. The operation performed followed the description given by Sherrington in his *Text Book of Mammalian Physiology*. Both ganglia were removed through a median incision, the usual aseptic precautions being observed. Four cats were operated in this way and were examined according to the method outlined above after an interval of forty-five days had elapsed from the time of operation. The wounds had all soundly healed by first intention.

The immediate effect of the operation was to cause great constriction of the pupil and paralysis of the nictitating membrane. The pulse rate at once went up to 192 beats per minute. This lasted only for a brief period, when it fell to between 156 and 168, at which rate it remained constant until the animals were killed. At about the end of a week the pupils began to return to their normal size and the nictitating membrane to retract and no longer extend to the front of the eye. No other effects were observed. The animals were active in catching mice whenever the opportunity occurred.

A careful study of the hearts of two of them was made. The fullest use was not made of the others as our technique was not at first very satisfactory. The interpretation of the experimental results is very difficult. They will be discussed as particular points are referred to subsequently. So little work has been done on degeneration in the autonomic system that there is great doubt as to the manner in which these nerves degenerate; further, it is uncertain how long it takes to bring about their complete disappearance, even if such is their ultimate fate. Langley was of the opinion that post-ganglionic nerves when severed from their cells of origin became inexcitable in two to ten days and that they completely degenerated and disappeared in thirty days. Eugling (who studied the disappearance of the vascular plexus in rabbits, using the methylene blue stain) states that remnants of these nerves can be found when the interval after the operation is twenty days, but not when the interval is extended to sixty days. Lapinsky believed that all traces of these nerves disappeared at the end of the second month or at least by the beginning of the third. Boeke allowed thirty days to elapse in his experiments on the degeneration of the sympathetic endings in muscle. Our difficulty

arises from the fact that it is impossible to affirm that the richness of any nerve bundle in non-medullated nerves in the cardiac plexus is diminished as a result of the operation. (This does not apply to blood vessels.) The difficulty of such decision is enhanced by the fact that according to Müller at least 70 per cent. of the pre-ganglionic fibres of the vagus are non-medullated. Moreover it is very difficult to distinguish between the post-ganglionic processes of the cardiac ganglia and other fibres: for soon after they arise from nerve cells they assume the same form as other fibres. There is still the difficulty that removal of the stellate ganglia alone may be insufficient to remove all the post-ganglionic fibres of the sympathetic system: for in the cat some may come from the cervical region and possibly from the thoracic ganglia.

In all nerves of the heart (even when examined before they approach the cardiac ganglia) there are many fine non-medullated fibres that present along their course fine ovoid varicosities. These we were inclined to regard as the sympathetic fibres. Even if this is a valid assumption the fact remains that they are still present after removal of the stellate ganglion though perhaps diminished in number.

CARDIAC GANGLIA

Gaskell, Shumacher, and most recently Perman, have furnished detailed accounts of the origin and distribution of the extra-cardiac nerves. We have, therefore, confined our investigation to the ganglia and nerves after they have actually reached the heart.

Mollard summarises the state of knowledge at the time he wrote as follows. Of the frog he says one is able to substitute for the idea of the three classic ganglia of Remak, Bidders and Ludwig the knowledge, obtained by improved technique, particularly by Dogiel, that the heart of the frog is provided with ganglion cells more or less numerous in all its parts, even extending right to the apex of the heart. The same holds also for other Amphibia and for the heart of Reptilia.

In mammals, says Mollard, we come to the same conclusions as in the frog. The heart of mammals is provided with ganglia in all its parts. They are most abundant in the region of the auricles. All physiological deductions based on the supposed absence of ganglia from certain regions of the heart are therefore subject to error. The progress of technique continually enlarges the field of the heart in which nerve cells are to be found. Dogiel investigated the heart of man, many common mammals, the frog and the tortoise. He found ganglia small and large and in great numbers in the plexus on the auricles; they are immediately subpericardial or even in the interstices of the muscle. In the ventricle he found them only rarely and then always in the neighbourhood of the auriculo-ventricular sulcus.

Smirnow declared that in all regions of the ventricles of the calf and the dog there are nerve cells even to the apex of the heart. An examination of

Smirnow's figures suggests to us that much of his material was not vital enough to give a differential staining with methylene blue and that he may have been misled in his identification of nerve cells. Claims for the confirmation of his results by others who used silver staining are also open to grave objection since connective tissue cells may be stained and if these lie in juxtaposition to nerve fibres the identification becomes exceedingly difficult.

As Perman (whose paper appeared in 1925) has given a summary of the literature, including the papers that have appeared since the monograph of Mollard, we will use his summary except for the papers which we mention in the bibliography.

Eiger finds numerous ganglia on the dorsal auricular wall, on the right of the superior and inferior venae cavae and on the left pulmonary veins. They are limited distally by the auriculo-ventricular sulcus. Numerous ganglia are found around the openings of the great veins and in the neighbourhood of the sulcus coronarius. Isolated ganglia are found in the neighbourhood of the auriculo-ventricular sulcus on the ventricle. All the ganglia lie in the subpericardial tissues, none in the myocardium.

Lissauer found that the ganglia were limited by the auriculo-ventricular sulcus and that none were present in the myocardium.

Fahr (1910) made a reconstruction of the heart of a child aged ten days. He found the ganglia most abundant in the auricular plexus. He figures ganglia on the septum between the two auricles, around the origins of the great veins and at the opening of the coronary sinus in the region of the node of Tawara. In the proximal third of the interventricular furrow he places some large ganglia. The ganglia were always included in the nerve plexus and were always subpericardial.

Aschoff arranges the ganglia in three groups: (1) one at the opening of the vena cava superior in the region of the Keith-Flack sino-auricular node, which he names the sino-atrial ganglion; (2) another on the dorsal wall of the auricle in the region of the interatrial septum, which he names the atrio-ventricular ganglion; and (3) a third at the basis of the great arteries, which he names the ganglion of the bulbus aorti.

The results of Perman were obtained by using a macroscopic method in an investigation of thirty human hearts. His macroscopic results agree with those of His and Fahr: he finds the posterior surface of the auricles and the roots of the great vessels studded with ganglia. He found the ganglia always interpolated in the nerve trunks, a fact, he says, that physiologists tend to overlook. He divides the ganglia into groups: one lying against the aorta and the pulmonary artery and extending on to the proximal ventricular wall; and a second group lying on the posterior surface of the auricle and extending again on to the proximal part of the ventricle. The first group belongs to the nerves passing ventral to the transverse sinus and supplying the ventral surface of the heart; the other to the posterior nerves which run behind the

transverse sinus and reach the auricles and greater part of the dorsal surface of the ventricles.

Perman finds that the ganglia always occupy the subpericardial tissues, which are important in pericarditis. He further believes that the arrangement of the ganglia is substantially the same in man as in such mammals as the dog and the calf, viz. a group belonging to the nerves that innervate the ventral ventricular surface and a group that innervates the auricle and the dorsal surface of the ventricle.

In a large number of animals Morrison, Meiklejohn and Oppenheimer have demonstrated the presence of nerves in the sinus node. In Tawara's node Wilson and Fahr have shown the presence of ganglion cells in the Artiodactyla. In man Aschoff and Fahr have demonstrated the presence of numerous ganglion cells about both nodes. Meiklejohn finds very few nerve cells in the bundle of His in Carnivora.

Perman believes he has been able to trace a branch twig from the nerve that supplies the right auricle to the sino-auricular node, but has not been able to find any ganglia in it. It has been found experimentally that the Keith-Flack sino-auricular node is stimulated by the right nerves and the Tawara node by the left nerves (Rothberger and Winterberg).

PERSONAL OBSERVATIONS

The method we used throughout this investigation was staining with methylene blue. By combining this staining with the process of clearing used in the Spalteholtz method we were able to make transparent preparations of the whole of the surface of the heart. The figures represent the results obtained by this method. The whole of the visceral pericardium with a stratum of the underlying muscle was stripped off from the surface of the ventricles. Further, the dissection was continued so as to include the whole of the auricles, the great veins and the origin of the great arteries. The piece was then spread flat and studied as a whole. An attempt was then made to plot the distribution of the ganglia and the nervous plexus. This sufficed for the larger elements. The finer elements were then plotted by the study of smaller pieces, which were sectioned by hand and studied piece by piece under the microscope. From the study of the heart of the snake, rabbit, cat and dog we find the distribution of the ganglia to be as follows: ganglia about the origins of the greater arteries and actually extending on to the beginning of the trunks of the pulmonary artery and on to the beginning of the ascending aorta.

The anterior face of the left auricle (where it lies posterior to the ascending aorta) is provided with numerous ganglia. They are also found extending to both auricular appendages. Over the posterior surface of the left auricle they are particularly abundant, and there extends along the interatrial septum a very large chain of ganglia. These lie in the region of both the sinus node and the auriculo-ventricular node. Several large ganglia are found in the neighbourhood of the auriculo-ventricular sulcus. This, however, in the animals we

have studied seems to form the caudal limit of their extent except in the heart of the snake, where collections of ganglia are found in the region of the posterior interventricular sulcus. The ganglia vary in size from those easily seen in these preparations by the naked eye to those so small that they are only found when thin sections are studied by the aid of the microscope.

By similar methods we examined the subendocardial plexuses of the right and left ventricles, but were unable ever to find in these positions any nerve cells either singly or in groups.

The position of these ganglia is almost entirely subpericardial. Some are nearer the surface than others: but in no case could their position be described as intramuscular. The rich plexus on the interior of the auricles, particularly in the region of the auricular appendices, was similarly examined: but in no case did we succeed in finding nerve cells on this plexus. In general our results are in agreement with those of the majority of observers, who limit the ganglia to the cranial side of the auriculo-ventricular sulcus and find no ganglia in the ventricles. That is, we are unable to confirm the work of Smirnow, who found ganglia even as far as the apex of the heart, and of Dogiel, who gave them a more modest distribution but insisted that they were to be found intramuscularly.

Two other points seem to be of importance. Firstly, the ganglia are far more numerous, particularly on the posterior surface of the auricles, than the published figures would lead one to believe. This is exemplified in the sketch of the heart of the snake. Secondly, the study of the distribution of these ganglia in sections of the whole of the superficies of the heart revealed so many ganglia of microscopic size that it was soon found impossible to represent them individually; hence a convention was adopted of the area to be covered. The picture gives very little idea of how very numerous ganglia are.

In fig. 1 is illustrated the heart of the common grass snake. The specimen was stained and cleared as a whole and the dorsal surface drawn to represent the appearance revealed by the aid of the binocular microscope. Numerous ganglia are found along the superior and the inferior venae cavae, and particularly about the sinus venosus. Ganglia also occupy the auriculo-ventricular sulcus and, as an exception to what we have found in mammals, they extend along the dorsal interventricular furrow in close association with the blood vessels. This is the only heart in which we have found the ganglia on the caudal side of the auriculo-ventricular sulcus.

DESCRIPTION OF THE PERICARDIUM OF THE DOG

The heart having been injected with methylene blue as already described, the pericardium was divided down the centre, beginning in front at the pulmonary artery.

The pericardium, including a superficial layer of ventricular muscle, was stripped off the ventricles and the whole of the auricles were removed. The

great vessels were laid open and the whole preparation made flat. It was fixed and cleared in the usual way.

A sketch was made to show the relative position of the various parts of the heart and great vessels and a rough drawing of the larger nerves was then plotted in. When this had been done the heart preparation was divided into small areas and these were sectioned by hand and examined microscopically piece by piece and the observations plotted on the chart. There is on the

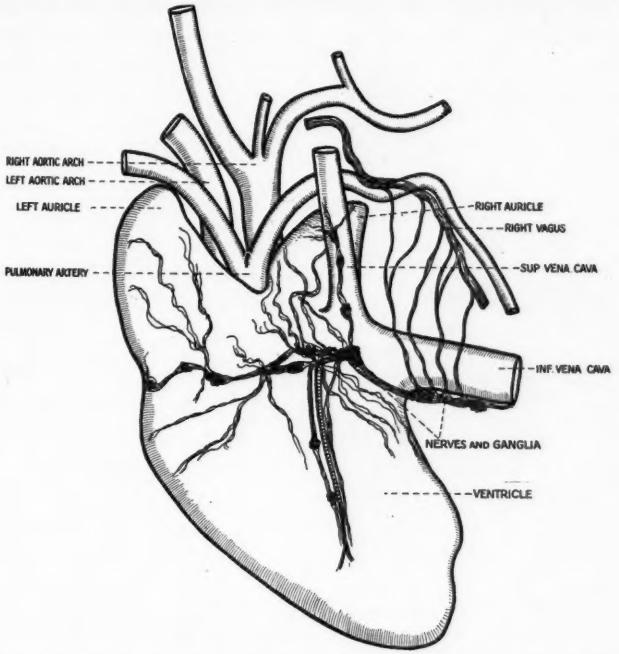

Fig. 1. Distribution of the nerves and ganglia on the dorsal surface of the heart and great vessels of the snake. All figures are drawn from methylene blue preparations.

external surface as well as on the internal surface of both auricles and ventricles an epicardial and an endocardial plexus. The larger incoming nerves are abundantly distributed, in particular about the left auricle. In addition a great many come down on the posterior border of the right auricle alongside the superior vena cava.

The nerves in their distribution to the interior of the heart follow the branches of the coronary arteries, forming around them the most extraordinary spiral rings. At various points the nerves leave the vessels and pass deeply into the substance.

The distribution of the ganglia was plotted out. It will be observed that they are found in clumps about the surface of the posterior aspect of the left

auricle, near the interauricular septum and around the face of the left auricle where it lies behind the ascending aorta. They are found as innumerable scattered clumps of cells. They are perhaps most abundant about the origins of the right and left coronary arteries. No nerve cells have been found in the ventricle. None have been found in the interior of the heart. The distribution of the endings of medullated nerves is also indicated. It will be observed that they are abundant on the ascending aorta and that moreover they are to be found in the connective tissue on the surface of the left auricle.

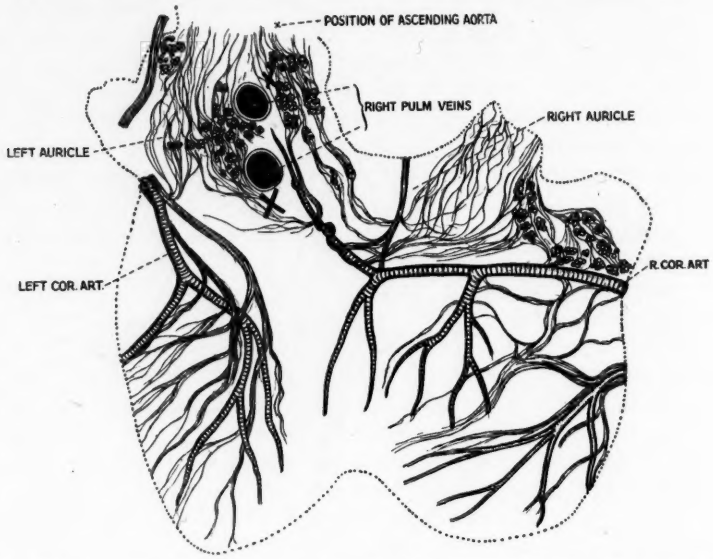

Fig. 2. The intracardiac nerve plexuses and ganglia of the heart of the dog. The visceral pericardium and adjacent layer of muscle were off the surface of the heart. The auricles and great vessels were included in the dissection and the whole mass was spread flat and drawn with the dorsal surface uppermost. X indicate the position of the medullated fibres with the afferent endings.

The following description is based on the heart of a cat which was stained with methylene blue and then figured before any fixation was carried out. The staining gave a perfect picture of the nerves of the heart, the nerves and the ganglia standing out in the greatest clarity. Ganglia varying in size from a pin's head to 6 or 7 mm. were evident in the following positions: (1) on the posterior surface of the left auricle. They are here in the greatest number and six distinct groups of nerve cells could be identified under the binocular. The cells are for the most part of small size, usually elongate or ovoid in shape and the nerves approaching and leaving them are easily picked up.

(2) Nerve ganglia small in size are found along the interatrial septum.

(3) Numerous small groups of nerve cells are found on the lateral surface of the right auricle.

(4) Three or four small groups are present on the anterior face of the left auricle behind the ascending aorta.

(5) Buried in the auriculo-ventricular sulcus especially in relation with the two coronary arteries are groups of nerve cells.

The nerves reach the heart in two main streams in the dog and the cat. One descends behind the upper border of the left auricle and spreads out as it descends. The large nerve trunks of which it is composed descend towards the auriculo-ventricular sulcus. Some of the smaller trunks to which it gives origin are interrupted by the outlying ganglia on the posterior surface of the

Fig. 3. Distribution of the ganglia on the heart of the cat: drawn from the right side.

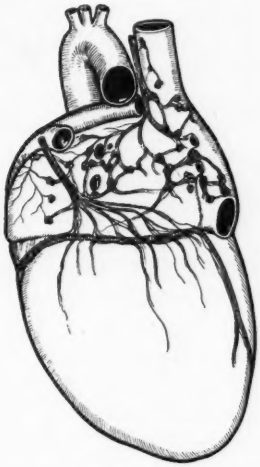

Fig. 4. Nerves and ganglia on the dorsal surface of the heart of the cat.

left auricle. The larger trunks composing this plexus descend towards the auriculo-ventricular sulcus and come into relation with the larger ganglia lying in the sulcus there. Moreover, some of the fibres of this plexus swing above and below the right pulmonary veins and contribute to the plexus which lies on the surface of the right auricle.

A second stream of fibres reaches the heart by passing across the superior vena cava. These fibres form a plexus on the surface of the right auricle and are there interrupted by several small ovoid or elongate ganglia. Out of this plexus a group of nerve fibres of fairly large size sweep towards the sulcus in the neighbourhood of the origin of the right coronary artery.

On the surfaces of the auricles mentioned in connection with the distribution of the ganglia there are in reality two plexuses to be distinguished. One

of these is composed of much larger fibres and is made up of the incoming fibres. The other, composed of much finer fibres, consists apparently of fibres which have come from the ganglia and are passing to their distribution in the auricle.

A similar arrangement has been confirmed in the dog by examination of thin slices of the auricular wall.

At the auriculo-ventricular sulcus all the nerve fibres belonging to these auricular plexuses appear to end. They bend inwards at the sulcus and from its distal border they pass to the ventricles, forming great spiral rings around the branches of the coronary arteries.

The operated animals (cats) presented no deviation from the above description.

Along the posterior wall of the left auricle it has been possible to trace large nerve bundles which have no ganglia upon them and can be followed across the auricle to the ventricle where they pass to their distribution. It is possible to examine such sections under the low power of the microscope and so closely investigate the composition and distribution of such nerves. The examination of these specimens suggests the existence of such nerve bundles, the absence of ganglia connected with them and their continuity to the surface of the ventricle.

Taking small portions of such nerves it is seen that they consist of small fibres which in addition are beaded, and of larger fibres which are smooth and regular in contour. They appear to have, at any rate in a proportion of them, a fine medullary sheath.

We have observed in the heart of the guinea-pig similar bundles, which appear to travel across the auricle to the ventricle without being interrupted by ganglia.

The operated animals present a similar arrangement in the nerve plexus and distribution of the ganglia and we believe that the fibres going to the ventricles are less rich in the finest non-medullated fibres.

TYPES OF GANGLION CELLS

The cells have been classified, particularly by Dogiel and Michailow. Dogiel divides these cells into three classes while Michailow divides them into four.

There are no essential differences between these classifications. The basis of the differentiation rests mainly on the differences of form of the dendrites.

The first type is the common round polygonal cell feebly staining and studded with from three to ten dendrites which are short and often varicose. These cells give off a non-myelinated fibre which can sometimes be traced to the muscles. We can confirm this description in detail. Such cells are figured drawn from a section of these cells in the subpericardial tissues of the dog's left auricle.

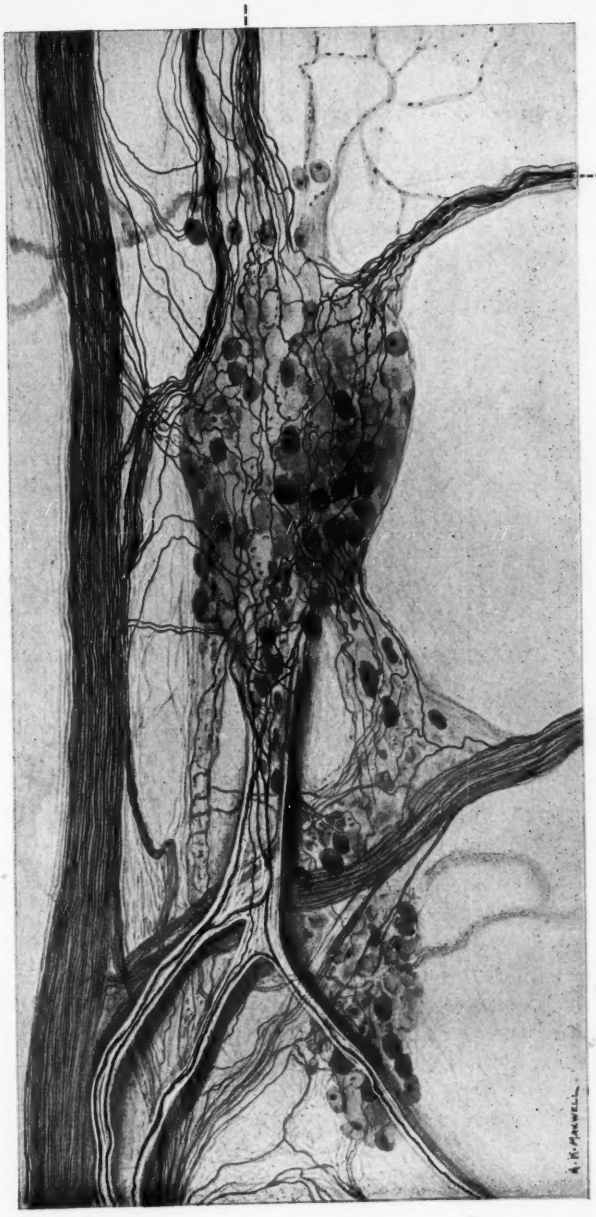

Fig. 5. Drawing of the general relationship of nerve trunks, ganglia, pre-ganglionic and post-ganglionic fibres. Dog.

A second type of which we have seen numerous examples is a cell that is often found singly embedded in a nerve trunk or again lying just adjacent to a bundle of fibres. The dendrites of these cells often extend for relatively great distances. The axis cylinder given off from this type of cell is often medullated for a quite considerable distance, the sheath then disappearing. This type is recognised by both the observers mentioned above. Dogiel was uncertain of its termination but certainly some of the axis cylinders of this type end in the cardiac muscle, as we have been able to follow individual fibres from the cell to the muscle. We can confirm his statement that these cells are often unipolar.

Fig. 6 A. Most common type of ganglion cell with capsule and pericapsular nerve terminals. Dog. 1/6 objective.

Another type is only a variant of the first type in which some of the dendrites given off interlace with adjacent cells and serve possibly to integrate the activity of the cells as a group.

Michailow described a cell which he called the rosette type. These are rare cells, which we have observed only once or twice, in which short dendrites are so arranged around the cell as to give it the appearance of a rosette. The axis cylinder appears to be a non-medullated fibre which joins the nerve bundle and appears to go to the muscle, but of this we are not certain. The interesting point is that in addition to the dendrites already described there is a long single dendrite drawn out into a long single process which extends for a considerable distance and then ends in a complicated end net which resembles very closely the sort of ending that is found at the termination of the medullated fibres. This ending lies quite free and is not in contact with

other fibres or cells. As a matter of fact it lies quite free in the connective tissue and it is hard to resist the idea that it is a sensory ending. What its

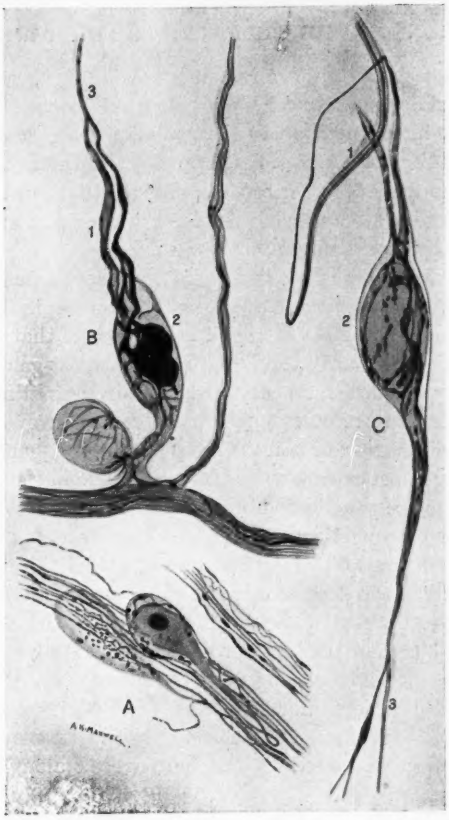

Fig. 6 B. Different types of nerve cells from the dorsal surface of the left auricle of a cat from which both stellate ganglia had been removed forty-five days previously.

A. Nerve cells lying included in a nerve trunk with pericapsular nerve terminals and apparently of the unipolar type.

B. An outlying nerve cell with pericellular nerve terminals (2) and elongated dendrite (1) stretching out into the tissues along with the post-ganglionic fibre (3). The post-ganglionic fibre could be traced to a muscle fibre.

C. An isolated nerve cell with a strongly medullated nerve fibre. Ending in a pericellular net around its body (2). The dendrites are elongated and run for some distance with the post-ganglionic fibre (3). The post-ganglionic fibre could be followed for a very long distance but was finally lost in the connective tissue.

function may be is very difficult to suppose but at once the idea comes to the mind that it may be the basis of an intracardial reflex.

The operated animals present no feature in the cardiac ganglia which distinguishes them from the normal animal.

THE RELATION OF THE CELLS TO THE INCOMING NERVES

In the incoming fibres to the ganglia it is possible in these preparations to follow a large bundle of fibres for a considerable distance and watch their gradual alteration in composition as they subdivide and become intercepted by the ganglia. The multiplicity of the ganglia and their distribution in the course of the fibres renders very probable the idea that most of the incoming fibres make connection with nerve cells. It is of course not possible to prove such a statement by morphological analysis.

If a favourable trunk is studied not long after it has been prolonged along say the posterior surface of the auricle it is possible to discriminate at least three varieties of fibres. It might be supposed that the general rule that pre-ganglionic fibres are medullated and that post-ganglionic fibres are non-medullated would furnish an easy means of discrimination. However, the exceptions to this rule are so frequent as to render it of little value. For often pre-ganglionic fibres are non-medullated and post-ganglionic fibres are medullated. A much better difference seems to reside in the fact first noticed by Gaskell that the pre-ganglionic fibres are larger than post-ganglionic fibres in the proportion of roughly 4μ to 1μ. In the incoming fibres there are obvious medullated fibres on which can be recognised the nodes of Ranvier. Such fibres constitute the depressor nerve of the vagus. There are also large fibres of uniform outline but without a medullary sheath. Such can often be traced to the nerve cells of the intracardiac ganglia. On the other hand, such fibres can often be identified arising from the nerve cells. However, all such fibres are not post-ganglionic nor do the fibres of the post-ganglionic group retain this large and uniform character for long. As they approach their termination they become exceedingly fine and exhibit along the fibre characteristic small swellings.

The third type is to be found as soon as the nerve bundle is examined after it arrives on the posterior surface of the auricle. This fibre is characterised by being very much finer than the other types and presents along its course numerous small beaded swellings.

This fibre can be seen in every part of the heart in the subepicardial and subpericardial plexuses and in the nerve plexuses of the auricular and ventricular muscles. All these types are to be observed in the operated animals. There is however a diminution of the third type. This is best seen when the nerves are examined just where they reach the posterior surface of the auricle. The fact that the operation was confined to the removal of the stellate ganglia and left untouched those fibres which come from the lowest cervical ganglia may account for the presence of some of these fibres. Furthermore, many of them may well be non-medullated fibres in the vagus. So far as we are dealing

with the cardiac nerves before they have entered into relationship with the cardiac ganglia we think that we can affirm that most of the fine beaded type

Fig. 7. Subendocardial nerves from the left ventricle of the dog. There is a plexus formed of large nerve bundles and another finer one composed of individual fine beaded fibres. The larger nerves are composed of thick uniform and fine beaded fibres.

belong to the thoraco-lumbar outflow. However, this distinction is of no value when we come to compare the post-ganglionic fibres of the vagus with

the sympathetic fibres. This applies absolutely when the fibres from the ganglionic have proceeded some little distance from their cells of origin.

THE MODE OF ENDING OF THE PRE-GANGLIONIC FIBRES

These fall broadly into two types, the pericapsular and the pericellular. In the former the fine varicose endings of the incoming fibre appear to be applied to the capsule that invests the nerve cell. In the second they are directly applied to the body of the cell and to its dendrites. These cells with

Fig. 8. Shows the curious manner in which the nerve bundles of the heart form spirals around the branches of the coronary arteries.

the pericellular investment stain much more deeply than do the pericapsular form. In the case of those cells in which the dendrites are relatively enormously prolonged the endings of the pre-ganglionic fibres wrap themselves around these elongated dendrites and so their endings become similarly protracted. We can confirm the statement of other observers that the incoming fibres when they have lost their myelin sheath divide in a variety of ways and often make connection with several ganglion cells.

In discussing the nerve fibres which terminate in the ganglia, Mollard says that they are of two kinds, one from the sympathetic system which may be medullated or non-medullated, and the other type of cerebro-spinal origin which is exclusively medullated. It may be remarked that His junr. regarded these cardiac nerve cells as belonging to the sympathetic nervous system. Though such an idea has found no support in recent times yet in Tandler's *Anatomy* the inconstant ganglion of Wrisberg in the superficial cardiac plexus of human anatomy is regarded as being of the sympathetic type.

In examining the figures of all other workers who have used methylene blue it is easy to see in their figures the fibres that we have called sympathetic.

Fig. 9. Drawing of the subendocardial nerve plexus of the left ventricle of the dog. It shows (1) the different types of nerve fibres composing the nerve fascicles, (2) fine beaded non-medullated nerve fibres in relation with connective tissue cells, (3) Purkinje cells with a nerve fibre lying on them.

However they (and in particular Dogiel) believe that they end in relation with the ganglia. This we cannot confirm either in the operated animal or in the normal animal.

Mollard is of the opinion that those nerves which form pericapsular endings belong to the sympathetic system and that these cells give off fibres which go to the muscle, while those which form the pericellular endings belong to the parasympathetic system and that these cells give off the cardiac-inhibitor fibres.

The same sort of idea is to be found in Müller's book, viz. that the cardiac

ganglia belong to the sympathetic as well as to the parasympathetic system. Embryological investigation as to the origin of these cells is indefinite. In a recent paper on the origin of the cells of Aurebach's and Meissner's plexus of the gut, a closely allied problem, Erik Müller believes them to be of both sympathetic and vagal origin.

This morphological dualism has never been destroyed by the apparently unequivocal results of physiological investigation that these ganglia all belong to the vagus. Fukutake dismisses the morphological differences as being of no physiological importance. There is no doubt that these morphological differences do exist and we believe that they are of functional importance but what we do not know.

The illustrations (fig. 6 B) that we give of these types are taken from our experimental studies. They show that none of the types are in any way altered as a result of removal of the stellate ganglia. The cells and the pre-ganglionic fibres are in no way altered in form, or variety. No cells in any way give the impression that they or their connections have been changed by the removal of a large portion at any rate of the sympathetic outflow. There is then good morphological evidence for believing that all the cells no matter how they may differ in form and function all belong to the para-sympathetic system.

THE DISTRIBUTION OF THE POST-GANGLIONIC FIBRES

Fukutake discusses the literature on this question fully. He believes that methylene blue is the best of all stains as it leads to the least changes in the tissues.

The endings of the nerves in the heart have been variously described. Opinions are constantly undergoing modification. Ranvier believed that the nerves spin a plexus around the muscle fibres and that these give off quite short branches which end in the muscle substance. Again Hofmann (quoted from Fukutake) for instance has been quite unable to find these and believes that where a nerve appears to end it is only an artefact from the methylene blue. He believes that the nerve plexus about the muscle fibre is continuous. Hofmann finally says that the question whether the nerves end in the muscle cannot be settled by anatomical methods. Michailow finds the finest plexus about the muscle fibres and from these are given off endings to the interior of the muscle. Glaser describes an intracardial network and knobby endings in the epicardium and endocardium. It is doubtful what these endings may be.

There is no agreement among authors as to how the nerves end in the heart. Fukutake expresses his agreement with all later authors who claim that the nerve fibres never pass into the interior of the muscle fibres and end in them. He says that in the innervation of the bundle it would be interesting to know if the ganglia belong to the epicardial or to the intrapericardial system, if the muscle is actually innervated and if the sympathetic can be

distinguished from the vagus. He says that hitherto no investigation of this problem has been made. He himself has been unable to offer any solution. He finds in the Purkinje fibres the same relation to the nerves as elsewhere in the cardiac muscle, i.e. they are surrounded but not penetrated by the nerves.

PERSONAL OBSERVATIONS

The real object of our investigations was to discover the nature of the double innervation of the heart.

The assumption that the nerves, as they entered the heart, could be divided into pre-ganglionic and post-ganglionic, vagal and sympathetic, by their size and presence or absence of a medullary sheath, proved not to be well founded. The absence of such a distinction has made the experimental results difficult to interpret.

In the investigations already described of the heart in the snake, rabbit, guinea-pig, dog and cat the entering fibres exhibit the two types already mentioned. These incoming nerves form a great plexus on the surface of the left auricle. If we follow the bundles of nerves approaching the ventricle, it is possible to define along the posterior surface of the auricle certain bundles that do not bear upon them any ganglia, nor do they receive bundles coming from the axons of the nerve cells themselves. We have observed these bundles particularly in the cat and also on the posterior surface of the left auricle of the guinea-pig.

There would then be reason to suppose that a considerable number of fibres reach the ventricles without being relayed through the cardiac ganglia. It is difficult to be certain: but in no instance have we succeeded in tracing fibres direct from the ganglia into the ventricles.

Under the epicardium and endocardium of all chambers of the heart there is to be found a most robust plexus of nerves (see fig. 7). The internal plexus seems to be derived from fibres that penetrate from the surface of the heart along with the blood vessels, and more particularly enter from the sulcus in the region of the atrio-ventricular node. We would draw attention to the extraordinary way in which the nerves are related to the blood vessels. They spin and entwine themselves in great loops about the vessels. When suitable bundles are examined in these plexuses it is apparent that they are composed of different types of fibres. Some of the fibres are much thicker than others. The former are fairly numerous and may be estimated to constitute about one-third of the fibres present. Others are extremely fine fibres with tiny varicose thickenings along them. Between these two extremes there are fibres slightly thicker than the smallest ones, sometimes smooth, sometimes varicose.

When bundles entering the posterior surface of the auricles of operated and non-operated animals are compared it is probable that the finer varicose are much less numerous in the operated animals. However, they are still

numerous and seem to reach the same frequency when the fibres are gathered into smaller bundles and are examined nearer to their destination. This means that as the fibres of both systems are approaching their end they assume a similar external appearance and are no longer distinguishable. This is most true when the finer plexuses of the muscles of auricles and ventricles and of the endocardium and pericardium are examined. When the blood vessels are examined however in the operated animals, it is apparent that the immensely abundant fine plexus that is found in the midst of the muscular wall is almost entirely wanting. Only once or twice were these fine nerves found. We may assume therefore that the extirpation of both stellate ganglia after a period of six weeks leads to the disappearance of great numbers of the sympathetic fibres.

The distribution of the nerves that form the great subcardial plexuses may now be followed.

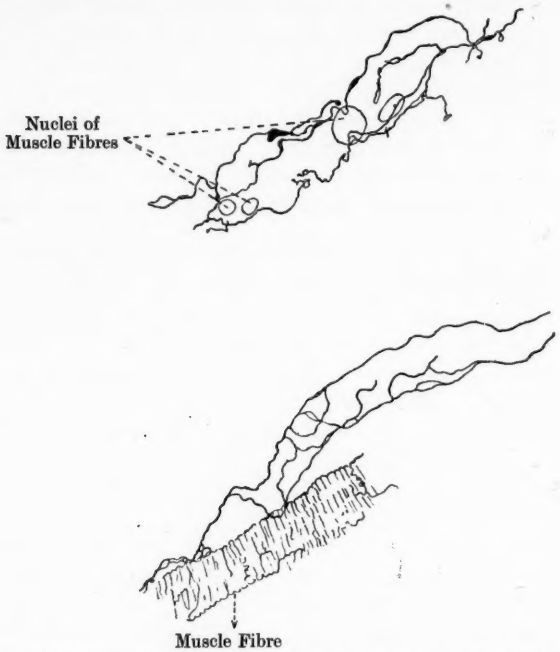

Fig. 10. Drawing of the intramuscular (pericellular) nerve plexus from the ventricle of a normal cat.

The nerve fibres form around the muscle fibres fine plexuses. On this point all observers are agreed. The discrepancy in opinion has arisen on the question whether this represents the final distribution of the nerves and if this plexus will account for the physiological phenomena of the heart. Much ingenuity has been displayed in maintaining the suggestion that it will.

In our sections stained with methylene blue we have succeeded in demonstrating that the fibres of this plexus ultimately penetrate the individual cells, and that they run in the actual protoplasm of the fibres and can be followed across the protoplasmic bridges joining fibres.

Here and there they give off little terminal twigs, which after a brief course end in little swellings or loops. It is interesting that recently Boeke has found this type of ending in cardiac muscle after staining with silver. We have further convinced ourselves of the intraprotoplasmic ending of the nerves by identifying them in cross-sections of the muscle fibre.

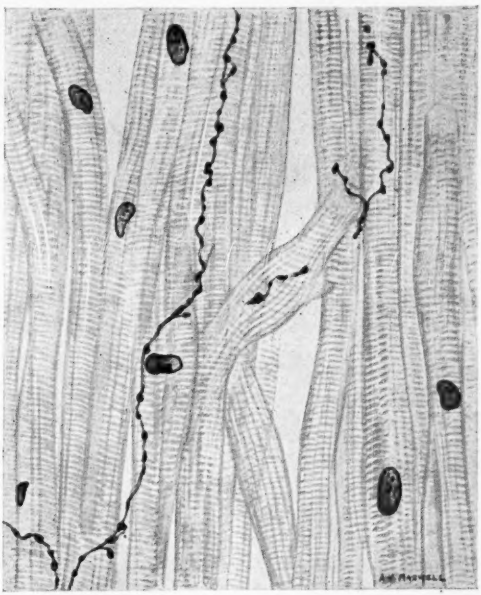

Fig. 11. Nerve fibres running intraprotoplasmatically; ventricle of the cat. Drawn under oil immersion lens and stereoscopic oculars.

Among the fibres forming the plexus and ending in the muscle in both auricle and ventricle only the fine and varicose type appears to be present. It is impossible at this point to draw any distinction between the fibres of parasympathetic and sympathetic origin.

In regard to the double innervation we may say that in the auricles it is possible to follow towards the muscle the nerve fibres that conform to the sympathetic type and also fibres that arise from the cardiac ganglia. Both types seem to reach the same perimuscular plexus, but it is no longer possible to distinguish between them.

It is also highly probable that the auriculo-ventricular bundle is supplied

by both types of fibres and, as all other workers have done, we have been able to identify groups of ganglion cells in the region of both nodes. In the Purkinje fibres which are apparent near the intraventricular surface of the heart the fibres we have seen on these cells are of the fine varicose form and therefore cannot be assigned to either vagal or sympathetic. We would remark that we have not succeeded in finding intramuscular endings in the elements of the bundle. In the operated cats we have been able to find the plexus about the muscle fibres and to trace a few fibres to the interior of muscle fibres. It is however in contrast to the normal cat and dog very difficult to

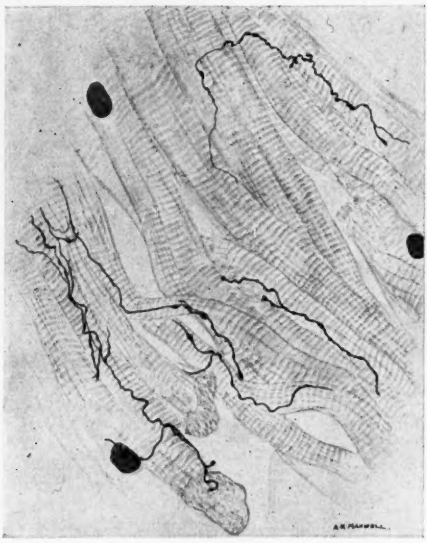

Fig. 12. Intraprotoplasmatic nerve fibres and endings from the left ventricle of a normal cat. Drawn as in Fig. 11.

demonstrate in the ventricles any intramuscular plexus. We have found as in the normal a subepicardial and a subendocardial plexus. Neither this nor branches from it were found reaching beyond the margin of the adjacent muscle. It is customary to assert that methylene blue is too capricious a stain on which to base any assertion that attempts to prove a negative. We believe this to be an exaggeration. Moreover we would affirm that it is the only method which can give results that are of use in a tissue like the heart. As we shall see when we describe the sensory elements of the heart these operated animals gave results that were the same as in the normal animals. We therefore believe from the experimental animals as well as from the study of normal animals that the main innervation of the muscle of the ventricles is by way of the sympathetic.

SENSORY ENDINGS IN THE HEART

We have found all muscular parts of the heart to be richly innervated (see figs. 7 and 9). In a similar way we have found all the non-muscular tissues to be richly innervated. In the subpericardial and endocardial tissues as well as in the valves of the heart we have found (as did Dr Morrison) abundant fine nerve plexuses. They are interwoven and composed of the finest fibres, which usually give off little branches that grow finer and finer

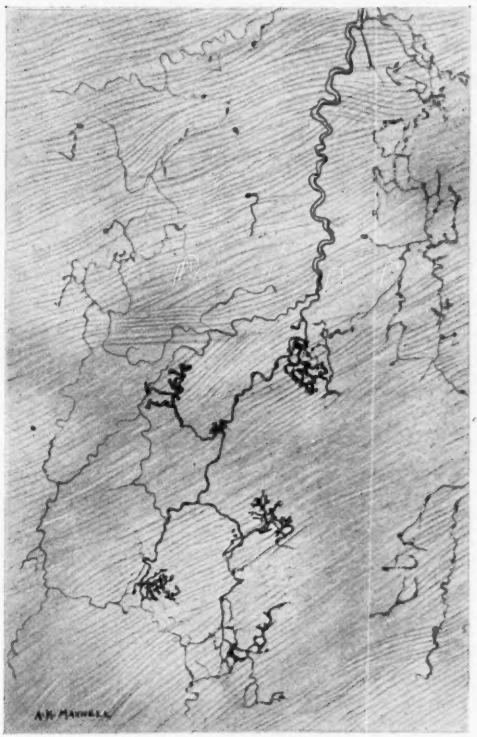

Fig. 13. Endings of medullated fibres at the boundary between the adventitia and media of the ascending aorta of the rabbit.

until they disappear. Occasionally little brushes of these fine fibres form a somewhat more complicated type of ending. Since these fibres innervate a part of the heart that is non-muscular presumably they can only be of an afferent nature. Furthermore, we find this plexus as abundant in the operated animals as in the non-operated animals. We therefore conclude (subject to the limitations on our operations already mentioned) that a great part of the

plexus must be derived from the vagus endings: indeed we have traced to it many of the thicker type of fibres. Just as in the muscular plexus, however, these fibres (as they proceed) grow progressively finer and ultimately become indistinguishable from any other type of fibre. This kind of plexus was described by Glaser.

One other point is worthy of mention. In the endocardium of the dog we have been confronted by large branching cells that give off fibres which sometimes proceed for quite long distances. These cells are sometimes independent but often enter into protoplasmic continuity with other cells of a like nature by means of their protoplasmic processes. These cells sometimes align themselves alongside of the capillaries. The cells stain diffusely and in fact are only stained by the methylene blue when the tissue is overdosed with the stain. The fine fibres in the plexus referred to often run alongside these cells and sometimes seem to be embedded in their protoplasm. These are connective tissue cells. It is apparent from the literature that they have often been described as nerve cells. The disposition of these cells and the relation of the nerves to them resemble very closely what Boeke has found in the cornea and the relation of the fine nerve plexus to the lamellar cells.

Fukutake did not succeed in finding the depressor endings, nor did he succeed in finding the sensory endings elsewhere in the heart. Michailow and Dogiel describe the sensory endings in the subpericardial and endocardial tissues of the heart, but Fukutake declares he has not seen them in any animal. Dogiel describes fine nerve endings about the fat cells. These we have seen also.

Dogiel and Smirnow have described in great detail the endings of medullated nerves. We can confirm their description. These have been followed both in the dog and in the rabbit and cat.

In the dog the fibres with their endings have been traced along the ascending aorta. They extend right down to the very beginning of the aorta in the neighbourhood of the semilunar valves and also on to the adjacent area of the auricle.

The medullary investment of the fibres is extremely easily seen and the fibres run for the most part independently and can be traced for long distances. Sometimes they are arranged in groups. The endings arise at the extremity of the fibre. As the nerve approaches its termination it gradually loses its medullary sheath and the naked axis cylinder extends for a short distance and then breaks up into a most complicated ending. The actual ending is extremely large and undergoes a most extensive subdivision branching and rebranching until a huge number of filaments are so produced; finally each filament ends in a bulbous expansion. The form of the nerves is practically the same in both the rabbit and the dog. The only difference is that in the dog the endings seem to be somewhat finer.

In the rabbit they have been traced as far as the origin of the great vessels and even along the beginning of their trunks. Their actual relation to the wall

of the vessel is such that after the fibres have run in the adventitia and approach their termination they bend sharply inwards and finally end in the adventitial sheet just superficial to the middle coat of the artery. In the auricular region they are confined to the neighbourhood of the aorta and there they behave in a similar fashion, actually ending beneath the epicardium and adjacent to

Fig. 14. Nerve endings (afferent) of medullated fibres in the left auricle of the dog.

the superficial muscle fibres, but in no case on the muscle fibres themselves. No such endings have been found in any other region of the heart. Though we are able to confirm in the main the description of these sensory endings and their extension over the surface of the left auricle yet we have not found them so widely distributed as Dogiel and Smirnow suggest.

INNERVATION OF THE CORONARY ARTERIES

The coronary arteries receive the richest innervation. In fact after examining many vessels we have found none more richly innervated than these. There is to be distinguished on the coronary arteries two types of nerves. The thicker fibres that we identify as vagal proceed to these vessels and end on the outer wall in adventitia without penetrating the muscular coat. It is

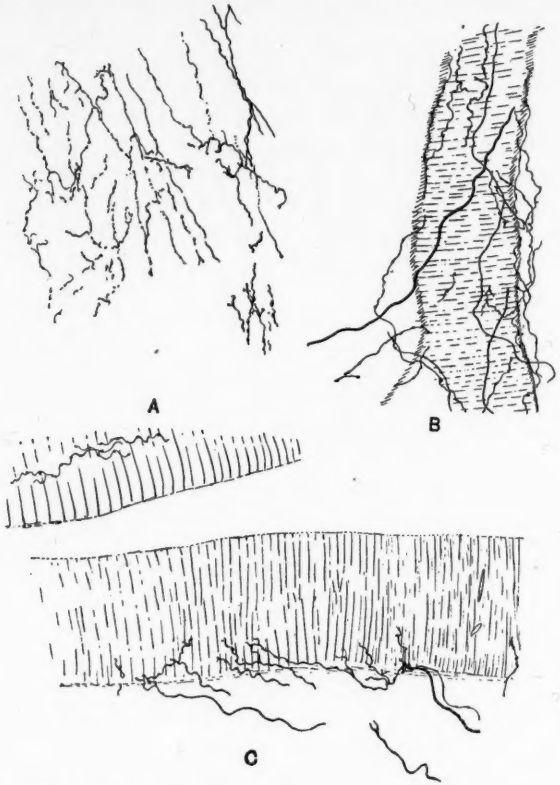

Fig. 15. Innervation of the coronary arteries.
(A) Rich intramuscular plexus (sympathetic) of a larger artery.
(B) Adventitial plexus containing both vagal and sympathetic fibres.
(C) Longitudinal section of the vessel showing nerve endings on the muscle fibres.

difficult to find the actual ending, which often seems to take the form of a swelling. Again they may become finer and finer until no longer visible. Branches can be traced to the artery from the nerve cells. In addition the muscular coat receives an enormously rich supply of the finest non-medullated nerves. These are beset with varicose swellings and they finally give off short

little branches that end on the individual muscle cells of the artery. These fine fibres can be traced to the precapillaries but as these grow smaller the nerves seem to cease. Hence it may be said that the finest capillaries are without any nerve supply at all.

In the operated animals the type of fibre we regard as vagal is still to be seen on the artery: but the sympathetic fibres have almost entirely disappeared, so that only a few were ever found. This confirms the opinion that

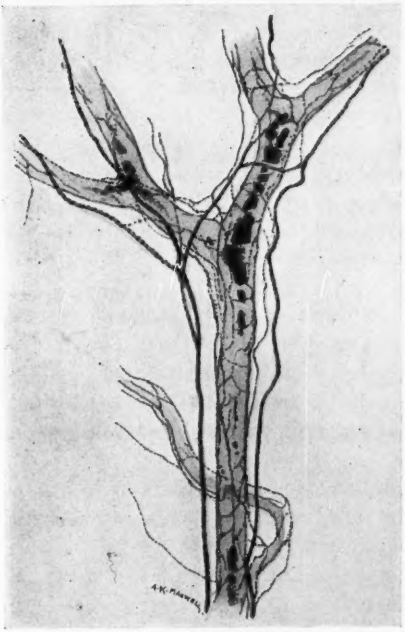

Fig. 16. Innervation of a tiny branch of the coronary artery from a cat with both stellate ganglia removed. The perivascular plexus about these tiny vessels must therefore be largely vagal.

the coronary arteries are doubly innervated. The adventitia receives the vagal fibres and the muscle receives a rich innervation from the sympathetic. This applies to the larger branches of the artery. When however the arterioles and the precapillaries are studied in the operated animals these are found to be invested by a fine plexus of nerves. These fibres must be in large part vagal since the larger arteries show the disappearance of the abundant plexus of fine nerves in the muscular coat. It would therefore seem that the larger arterial branches are innervated both by parasympathetic and sympathetic fibres, while the smallest branches are innervated predominantly by vagal

post-ganglionic fibres. This may throw some light on the widely divergent results hitherto obtained in physiological research on vaso-dilatation and vaso-constriction in the heart.

SUMMARY

(1) The intracardiac ganglia are limited caudally in animals such as the dog, the rabbit, the cat and the guinea-pig by the auriculo-ventricular sulcus.

(2) The type of cell though varying in disposition of the dendrites and in the mode of the ending of the pre-ganglionic fibres all belong to the parasympathetic system. The distinction between pericellular and pericapsular terminations of pre-ganglionic fibres is so definite as to suggest a difference in function.

(3) In the proximal course of the intracardiac fibres there can be distinguished two types of non-medullated fibres: one that is thicker and more uniform and may be pre-ganglionic, *or* post-ganglionic in part of its course; the other fine and varicose. The former belong to the parasympathetic, the latter to the sympathetic system.

(4) Both types when traced to their distributions either in the muscular or non-muscular tissue become indistinguishable. This makes the interpretation of degeneration experiments very difficult.

(5) Some evidence has been brought forward to suggest that the auricles and the auriculo-ventricular bundle are supplied by both parasympathetic and sympathetic fibres while the ventricular muscle is supplied by sympathetic fibres only.

(6) The fibres spin a plexus about the muscle cell and ultimately enter the protoplasm of the muscle and run in the protoplasmic connections of the muscle. Small endings often perinuclear in position are given off inside the muscle cell. In the auricles fibres from both systems appear to end intramuscularly.

(7) In addition to the endings of medullated nerves on the auricles and great vessels the non-muscular tissues are innervated by a very fine plexus of nerves, which in great part at any rate belongs to the vagus.

(8) The larger branches of the coronary arteries are mainly innervated by the sympathetic but their smaller branches are supplied mainly by the vagus.

(9) The larger branches of the coronary arteries are innervated by both systems but mainly sympathetic, but the finer branches mainly by the vagus.

In conclusion I wish to express my gratitude to Mr A. K. Maxwell, who drew the illustrations for me, and to Mr Randoll, who assisted me in the operations and the histological preparation of the material.

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ASYMMETRY IN HERMAPHRODITE PIGS

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INTRODUCTION

In this paper I describe two new true hermaphrodite pigs, and bring together all that I have been able to find out about asymmetry in the literature of such monstrosities. I wish to thank Professor J. S. Huxley for valuable advice on the physiology of asymmetry.

DESCRIPTION OF TWO NEW CASES OF TRUE HERMAPHRODITISM IN PIGS

The anatomy of the two new hermaphrodites is sufficiently well shown in figs. 1, 2 and 3 to render detailed description unnecessary.

Index to lettering of figures.

A	Anus	*MIC*	Ischio-cavernosus muscle
B	Urinary bladder	*MRC*	Retractor clitoridis muscle
BU	Bulbo-urethral gland	*MRP*	Retractor penis muscle
CnU	Cornu uteri	*O*	Ovary
CCC	Corpus cavernosum clitoridis	*OT*	Ovarian patch on testis
CCP	Corpus cavernosum penis	*Pa*	Pampiniform plexus
E	Epididymis	*R*	Rectum
F	Fallopian tube	*SpAE*	Sphincter ani externus
LC	Ventral labial commissure	*T*	Testis
MBC	Bulbo-cavernosus muscle	*U*	Urethra
MBG	Bulbo-glandularis muscle	*UO*	External urethral orifice
MCVe	Constrictor vestibuli muscle	*V*	Vagina
MCVu	Constrictor vulvae muscle	*VD*	Vas deferens

No. 10[1] has an ovary on the left, and an ovotestis on the right. The Graafian follicles in the ovary on the left are few and very large. The testis has the usual cryptorchid character. The vagina and uterus are almost those of a normal female, except that the cervix is ill differentiated internally. The Fallopian tube, which occurs on the left side only, is thicker than the normal structure.

[1] I have previously described two true hermaphrodites (Nos. 1 and 2) and seven "pseudo-hermaphrodites" (Nos. 3–9). See reference 1.

The external genitalia are those of a normal female except that the ventral labial commissure projects upwards rather further. The male accessory organs

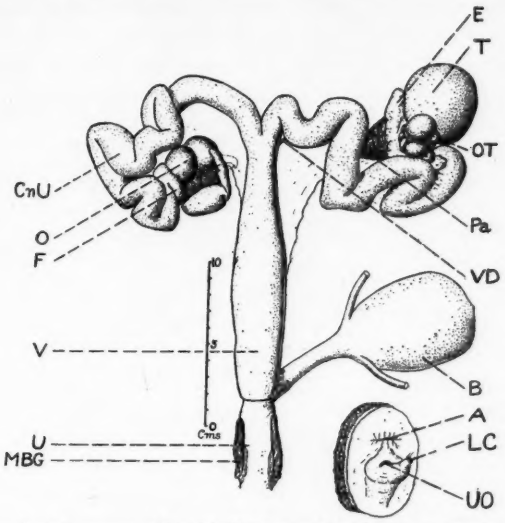


Fig. 1. Reproductive organs of No. 10. The internal genitalia are viewed from above.

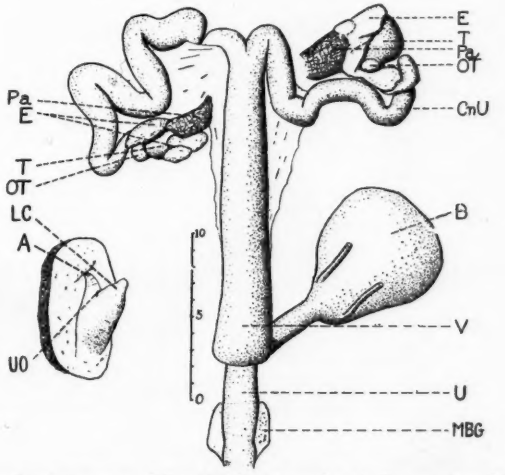


Fig. 2. Reproductive organs of No. 11. The internal genitalia are viewed from above.

consist of an epididymis, vas deferens, rudimentary vesicula seminalis, and pampiniform plexus on the right side only. On the left side there is no epididymis nor pampiniform plexus; but a Gartner's canal running along the

unpaired part of the uterus represents a vestigial vas deferens. A bulbo-

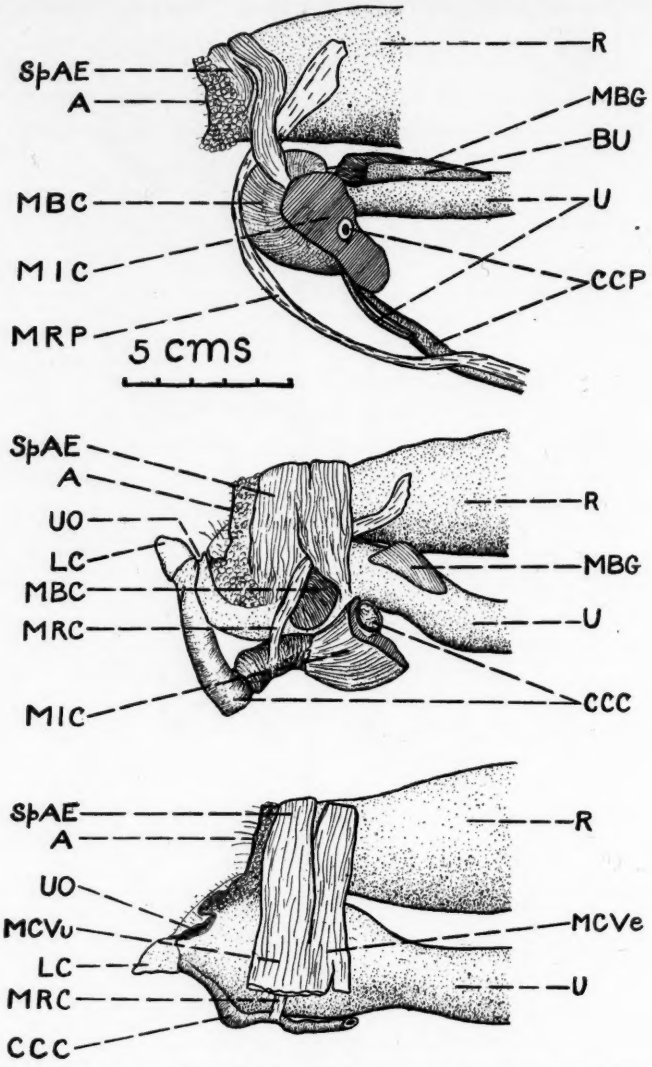


Fig. 3. Left side view of the urethra and adjacent structures of a normal (castrated) male (above), of an hermaphrodite (No. 11) (centre), and of a normal female (below).

glandularis muscle, characteristic of the male, is attached to the urethra on each side.

No. 11 has an ovotestis on each side, the ovarian part being larger on the

left than on the right, and the testicular part larger on the right than on the left. The ovarian tissue is degenerate, with few Graafian follicles and much fibrous tissue. The differences from No. 10 are that there are an ill-formed epididymis, a vas deferens, a rudimentary vesicula seminalis and a small pampiniform plexus on both sides, that the Fallopian tube is vestigial on each side, and that the opening of the vulva is reduced to a crescentic slit. The exact relations of the organs adjacent to the left ovotestis to one another are difficult to determine since they are closely bound to one another by an excessive amount of connective tissue.

Review of the Literature. In Table I, I have included every reference to a true hermaphrodite pig which I have been able to obtain. In the last column the word "right" or "left" appears, according to whether the right or the left gonad shows the greater proportion of testicular to ovarian tissue. The sign "0" indicates that neither side is appreciably more male than the other. The sign "–" indicates that on account of unilateral castration or unilateral gonad deficiency it is impossible to say which side should be regarded as more male than the other. The sign "?" indicates that I have been unable to obtain the paper in which the specimen was described, and that no other paper known to me refers to it in sufficient detail to enable one to say on which side the proportion of testicular tissue was greatest.

The table shows that five specimens have been described with an ovary on the left side and a testis on the right, but only one with the reverse arrangement. Further, three specimens have an ovary on the left and an ovotestis on the right, and only one has a testis on the left and an ovotestis on the right.

Table I.

Author	Reference	Left gonad	Right gonad	Which side is the more male?
Gould	7	Ovary	Testis	Right
Gurlt	8	Ovary	Testis	Right
Kingsbury	9	Ovary	Testis	Right
Reuter	13	Ovary	Testis	Right
Pick 5	11	Ovary with a few seminiferous tubules	Testis	Right
Baker 1	1	Ovary	Ovotestis	Right
Baker 2	1	Ovary	Ovotestis	Right
Baker 10	This paper	Ovary	Ovotestis	Right
Baker 11	This paper	Ovotestis	Ovotestis	Right
Garth 1	6	Ovotestis	Ovotestis	Right
Pick 3	11	Ovotestis	Ovotestis	Right
Kopsch and Szymonowicz	10	Ovotestis	Ovotestis	0
Becker	2	Ovotestis	Ovotestis	?
Walentowicz	15	Ovary and testis	Ovary and testis	?
Pick 1	11	Ovotestis	Ovotestis	Left
Pick 2	11	Ovotestis	Ovotestis	Left
Sauerbeck	14	Testis	Ovotestis	Left
Corner	4	Testis	Ovary	Left
Garth 2	6	Castrated	Ovotestis	–
Pütz	12	No gonad	Ovotestis	–
Pick 4	11	Ovotestis	Castrated	–
Duchanek	5	?	?	?

The conclusion to be drawn from the table is that in hermaphrodite pigs the left gonad is usually an ovary or ovotestis, while the right gonad is usually a testis or ovotestis.

THE SPACIAL RELATION OF OVARIAN TO TESTICULAR TISSUE IN OVOTESTES

In each of my four specimens the ovarian part of the ovotestis occurs in the same place in relation to the testis and adjacent structures. This is apparent from a consideration of figs. 1, 2 and 4. In these figures the right gonads are all seen from the same point of view, which is arrived at as follows: The internal genitalia are placed dorsal side uppermost. The gonad and attached parts are

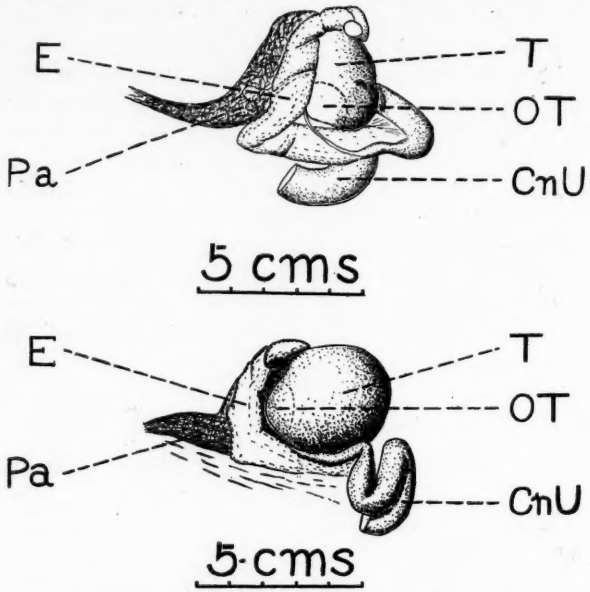


Fig. 4. The right ovotestis and adjacent structures of hermaphrodites Nos. 1 (above) and 2 (below).

then moved forward ventrally beneath the uterine cornu and brought up again in front of it, so that they are now seen in ventral view with the originally posterior end appearing anterior. When this is done, the epididymis appears L-shaped; the vestigial Fallopian tube runs along the horizontal part of the L and loses itself between the vertical part of the L and the gonad; and the pampiniform plexus projects (in a right ovotestis) to the left of the vertical part of the L. The ovarian tissue now appears in each case in the same place, namely on that part of the testis which is nearest to the bend of the L of the

epididymis. In other words, the ovarian patch is situated on the ventro-antero-median surface of the testis. Apparently the corresponding part of the embryonic gonad gives rise to ovarian tissue more readily than the remainder.

When the amount of testicular substance is small and the epididymis ill formed or absent (as for instance in the case of the left gonad of No. 11) it is not possible to check these relations.

THE PHYSIOLOGY OF THE ASYMMETRICAL DEVELOPMENT

The primary asymmetry of the body, which gives rise to the asymmetry of the gonads, might be due either to gynandromorphism or to some difference in metabolism between one side of the body and the other. The first alternative is unlikely, for if irregularities in sex-chromosome distribution were the cause, neither side would tend to be male more commonly than the other. The second alternative receives support from the case of Bond's pheasant(3), in which each tail feather was male on one side and female on the other—a condition which can hardly be accounted for by irregularities of sex-chromosome distribution.

When the gonads themselves are different on the two sides of the body, the accessory reproductive organs tend to exhibit a corresponding asymmetry, the male organs being best developed on the same side as the testis (or testis with ovarian patch), and the female organs on the same side as the ovary. This statement, which applies to the epididymes, vasa deferentia, vesiculae seminales, pampiniform plexus and Fallopian tubes, is based upon the data brought together in Table II, which shows the condition of these organs on each side of the body in the ten specimens which exhibit the most marked asymmetry in their gonads.

One is accustomed to think of the development of these organs as being conditioned by the gonad-hormones alone; but since the hormones must be carried equally to both sides of the body, it is clear that some other influence must be at work as well. This influence, whatever it is, must be one which is completely swamped by either gonad-hormone acting alone, but which has a chance to show itself when both ovarian and testicular hormones are present to counterbalance one another. Two possibilities present themselves as to the nature of the influence.

(1) The first possibility is that there is some such relation between the accessory organs and the gonad as exists between the lens and the optic cup in the developing newt.

This could be shown diagrammatically thus:

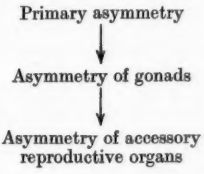
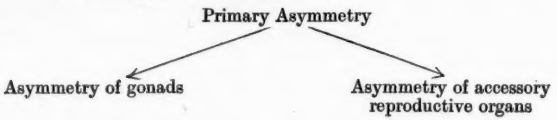


Table II.

	Left Side					Right Side				
	Female organs	Male organs				Female organs	Male organs			
	Fallopian tube	Epididymis	Vas deferens	Vesicula seminalis	Pampiniform plexus	Fallopian tube	Epididymis	Vas deferens	Vesicula seminalis	Pampiniform plexus
Gould (ovary on left and testis on right)	+	–	–	–	?	–	+	+	v	?
Gurlt (ovary on left and testis on right)	+	–	–	?	?	–	+	+	?	?
Kingsbury (ovary on left and testis on right)	+	–	–	?	?		+	+	?	?
Reuter (ovary on left and testis on right)	+	v	v	v	?	v	+	+	v	?
Pick 5 (ovary with a few seminiferous tubules on left and testis on right)	+	–	–	+	?	–	+	+	+	?
Baker 1 (ovary on left and ovotestis on right)	+	–	v	v	–	v	+	+	v	+
Baker 2 (ovary on left and ovotestis on right)	+	–	v	v	–	v	+	+	v	+
Baker 10 (ovary on left and ovotestis on right)	+	–	v	–	–	–	+	+	v	+
Sauerbeck (testis on left and ovotestis on right)	v	+	+	v	?	v	+	+	v	?
Corner (testis on left and ovary on right)	v	+	+	?	?	+	–	–	?	?

The sign "+" indicates that the organ concerned is present, the sign " – " that it is absent. The letter "v" indicates that the organ is vestigial.

(2) The second possibility is that the same influence that causes the gonad of one side to be male and of the other to be female also causes the accessory organs of corresponding sides to be male and female respectively. This possibility can be shown diagrammatically thus:



SUMMARY

1. The left gonad of hermaphrodite pigs is usually an ovary or ovotestis, while the right gonad is usually a testis or ovotestis.

2. The ovarian part of ovotestes is always in the same place in relation to the testis and adjacent parts. It is situated ventro-antero-medially to the testis, near the right-angle bend in the epididymis.

3. The epididymes, vasa deferentia, vesiculae seminales, pampiniform

plexus and Fallopian tubes tend to show an asymmetry corresponding with that of the gonads.

4. Some influence other than the gonad-hormones affects the development of the accessory reproductive organs. This influence is swamped by either gonad-hormone acting alone, but shows itself when both testicular and ovarian hormones are present to counterbalance one another.

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DESCRIPTION OF A HUMAN EMBRYO OF TWENTY-TWO PAIRED SOMITES[1]

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CLINICAL HISTORY AND AGE

A human chorionic vesicle was kindly presented to me in November, 1923, by Dr Mahfouz Bey, Professor of Midwifery at Kasr-el-Eini Hospital, Cairo. He gave me the following short history without dates: "Copulation took place 2 weeks after menstruation. Abortion occurred 5 days after the succeeding menstruation was due; haemorrhage two days before the abortion. The period

[1] Thesis approved for the Degree of Master of Science in the University of London.

between copulation and abortion is 18 days." Whether that was the only copulation between the two menstrual periods or the last before the abortion is not stated. If it was the only copulation, the fertilisation age of the embryo will be 17 days, or 15 days if the embryo ceased to grow after the haemorrhage which occurred 2 days before the abortion. If copulation had taken place preceding the one mentioned in the history, we fall back on the menstruation age for estimating the age of the embryo. This would be 37 days, taking the 2 weeks starting from the end of menstruation and adding 5 days, being the average period of flow.

The greatest length of the embryo measures 2·9 mm. and according to Mall's age curve, an embryo of 3 mm. long has 41 days menstruation age and 30 days copulation age, which is the probable age of this embryo when compared with other embryos of more definite age. According to His's curve, an embryo of 3 mm. long has copulation age of 17 days, which agrees with the age given in the history.

Peter Thompson, in describing an embryo of 23 somites and 2·5 mm. long, says that "it resembles in many ways His's embryo L.G. which was 2·15 mm. in length and estimated to be about 15 days old."

Davis described an embryo of 20 somites in which three copulations have taken place during two menstruations, and from his data he works out three copulation ages, the first 17 days, the second 24 to 27 days and the third 31 to 37 days, and he believes that the last is the right age of his embryo. He says:

The first copulation age (17 days) is too young to merit serious consideration, for by subtracting one day, as suggested by Triepel (1914) and Bryce and Teacher (1908), the fertilisation age would be 16 days, just one day older than the Bryce-Teacher specimen. Moreover, this coition occurred during the period in which, according to Siegel (1915) and Issmer (1889), intercourse is least likely to be fruitful. The probable fruitful coition, therefore, is reduced to the second or to the third preceding one. From the second we obtain a copulation age of 24 to 27 days, and from the third 31 to 37 days. According to the age curve of Mall (1918) a 3 mm. embryo should have a menstruation age of 40 to 41 days. By comparing the data at hand with this age curve, it is clear that the menstruation age of 42 days is probably the correct one. The copulation age according to Mall's chart would be 30 days. This falls between the possible copulation ages of 27 and 31 days, as shown in Table I, and may, therefore, be regarded as very close to the actual age of the embryo.

Johnson describes an embryo of 24 somites and he says the age of the specimen is uncertain from the data obtained, but it corresponds very closely to an embryo of 28 days as estimated by Mall.

Van den Broek describes an embryo of 22 somites but mentions no age.

The above-mentioned four embryos, Thompson's, Davis', Johnson's and Van den Broek's, resemble very closely this embryo, as will be shown later, and according to Mall's age curve they range in age between 28 and 30 days, which is more probable than the age of 15 to 18 days given to them by His's age data.

TECHNIQUE

The vesicle, which had been kept in spirit for some time before I received it, is oval in shape with a broad and a narrow pole. It measures 18 mm. in length and 13 mm. in diameter. It is evenly covered with villi excepting a small area on one side which is scantily covered. The embryo was attached to the inner surface on the side opposite this area. The vesicle was opened at the slightly villous area and the embryo with the attached part of the vesicle was cut out and transferred to formalin, then graded up through the alcohols, cleared in cedar-wood oil and embedded in paraffin.

The embryo measures 2·9 mm. in greatest length. It was cut transversely into 329 sections of 10μ each. The sections were stained with haematoxylin and eosin.

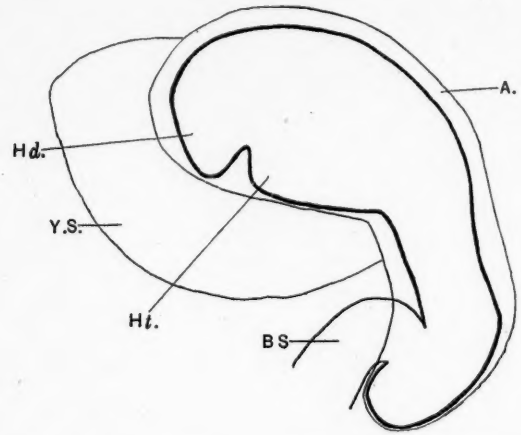


Fig. 1. Lateral view of the Embryo. *A.* = Amnion; *B.S.* = Body stalk; *Hd.* = Head; *Ht.* = Heart; *Y.S.* = Yolk sac.

The following observations were made in the Institute of Anatomy, University College, London, under the guidance of Professor J. P. Hill, to whom my gratitude is due for his advice and criticism, and kindness in allowing me to work in his Department.

Three models were made by the wax plate method, one of the whole embryo magnified 200 diameters with the left lateral wall removed, another of the brain and a third of the pharynx.

EXTERNAL FORM

Fig. 1, of the left lateral view of the embryo, shows that the head is large and slightly flattened cephalo-caudally and inclined to be pointed, in which it resembles that of Thompson's embryo.

Caudal to the head there is the large swelling of the heart separated from the head by the cleft-like mouth. The dorsum of the embryo gives the outline of a well-marked curve which can be divided into three portions. The first, the dorsal flexure, is the largest and extends from the head to a level caudal to the yolk stalk, with its convexity directed dorsally; the second (ventral flexure) extends from the caudal limit of the first to a level caudal to the body stalk; it is the smallest and its convexity is directed ventrally. This will place the ventral flexure at a level caudal to that of the yolk stalk, agreeing in this respect with Davis' and Johnson's embryos, and disagreeing with the description of His, who places the ventral flexure at the level of the yolk stalk. The third curve extends from the caudal limit of the second to the tip of the tail; it is intermediate between the other two in size and its convexity is directed dorsally.

The yolk sac is very large, nearly the same size as the embryo and is directed cranially and to the right side of the embryo, which appears to lie on it. The body stalk is thick and bends caudalwards. The amnion can be seen enveloping the embryo and there is a space between them, especially at the head end. This space is absent in Van den Broek's embryo, where the amnion is applied closely to the embryo.

In the model the above features can be seen. In the region of the head the optic vesicles are seen as two swellings, one on either side of the cephalic end of the head. Viewed laterally there are to be seen the three ectodermal grooves of branchial pouches, 1, 2 and 3. They are graduated in size, the 1st having the greatest vertical extent. These grooves mark out three visceral arches which are also graduated in size, the most cephalic or mandibular arch being the largest. The 4th visceral pouch, which is present in this embryo, has no corresponding groove on the surface, a condition also found in Thompson's embryo.

In apparent continuity with the dorsal ends of the 1st and 2nd arches there are two small swellings, one to each arch. These swellings correspond to the ganglia of the trigeminus and acoustico-facialis, the former related to the 1st and the latter to the 2nd arch. Caudal to the swelling of the acoustico-facial ganglion and close to it, there is the small opening of the otic vesicle which is in line with the second ectodermal groove. The branchial region appears normal and resembles the corresponding region in Johnson's embryo (24 somites), Thompson's embryo (23 somites), Van den Broek's embryo (22 somites), and Davis' embryo (20 somites).

A short distance behind the last ectodermal groove, the 1st somite appears as a bulging from the lateral wall of the embryo near the dorsal middle line. This is followed by regular swellings of the subsequent somites. The first three are large but not distinctly marked out on the surface. The rest become reduced in size towards the tail.

The yolk sac was accidentally detached from the embryo during the process of dehydrating. The yolk stalk is a very wide canal connected with the mid-gut.

At the tail end, the posterior neuropore is widely open. On the ventral surface of the embryo, at the tail end, there is a depression representing the anal pit and at the bottom of it the ano-cloacal membrane.

The body stalk comes out from the caudal third of the embryo. It is of large size and is bent caudally and to the right side of the embryo.

The embryo is twisted longitudinally with the head turned towards the right and the tail towards the left. The plane of the twist is in the middle of the mid-gut.

INTEGUMENT

The integument is generally of one layer of cubical ectodermal cells. It is thin on the dorsal surface over the neural tube where the cells are flattened in shape.

There is no indication of the lens primordium opposite the optic vesicles and a thin layer of mesenchyme still intervenes between the optic vesicles and the ectoderm overlying them. The ectoderm, which has folded in to form the wall of the otic vesicle, is formed of a thick layer of narrow columnar cells, and joins the surface ectoderm round the opening of the otic vesicle.

In the region of the branchial arches, the ectoderm is thickened and the cells are columnar in shape.

In the region of the oral cavity, the ectoderm is slightly thickened, forming the superficial layer of the bucco-pharyngeal membrane, which is perforated in two places. In the roof of the oral cavity, the ectoderm is in close apposition with the primitive infundibular recess of the fore-brain.

The ectoderm over the pericardial cavity is composed of one layer of flattened epithelium.

THE NERVOUS SYSTEM

The nervous system consists of the brain with its three main divisions, the ganglia of the Vth, VIIth, VIIIth, IXth, and Xth cranial nerves, the spinal cord and the ganglionic crest. The whole system lies underneath the ectoderm in the dorsum of the embryo and follows its curvature. Apart from a longitudinal slit which runs through the whole length of the neural tube, obviously an artifact due to shrinkage, the tube is closed except at its caudal end, where the posterior neuropore is still patent. In this feature it agrees with the embryos of Davis (20 somites), Van den Broek (22 somites), Thompson (23 somites) and Johnson (24 somites), but it disagrees with the Janosik embryo (24 somites), which shows a patent anterior and closed posterior neuropore, and Bremer's embryo of 4 mm. long whose neural tube is still open in front and behind. From this it appears that the order of closure of the neuropores varies, but in the majority of embryos the anterior neuropore closes first; and the stage at which closure takes place is at 20 to 24 somites for the anterior, and 30 somites for the posterior neuropore. Whether the delay of closure of the anterior neuropore or the reversal of order of closure is due to some abnormal condition of the embryos in which this occurs, or a variation of a normal condition,

cannot be definitely stated. Davis believes that closure of the anterior neuropore first is the normal condition, and he looks upon the failure of its closure as a delay of the normal process or possibly the result of a complete arrest of development.

The Brain. The primary divisions of the brain (fig. 2) are well marked. The fore-brain is a simple vesicle separated from the mid-brain by a slight groove on the outer surface. A small area at its cephalo-dorsal border is fused with the overlying ectoderm, marking the last point of closure of the anterior neuropore.

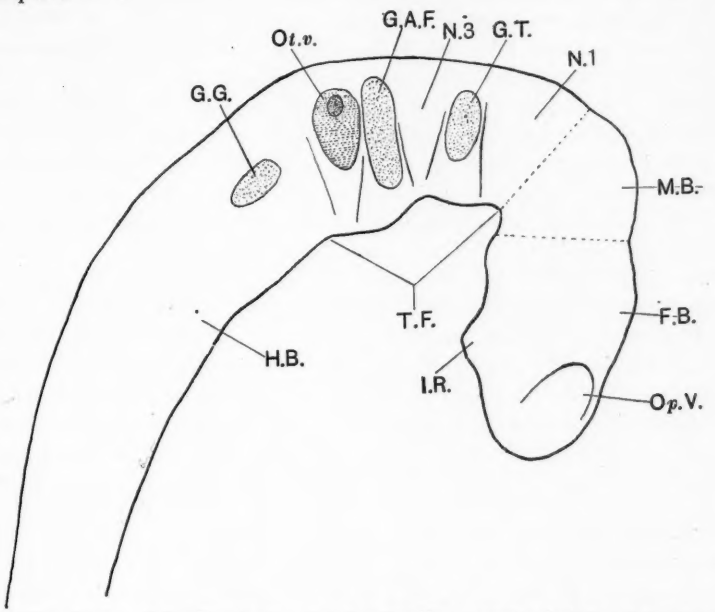


Fig. 2. The Brain. *F.B.* = Fore-brain; *G.A.F.* = Ganglion acoustico-facialis; *G.G.* = Ganglion glossopharyngeus; *G.T.* = Ganglion trigeminus; *H.B.* = Hind-brain; *I.R.* = Infundibular recess; *M.B.* = Mid-brain; *N.* 1. = 1st neuromere; *N.* 3. = 3rd neuromere; *Op.V.* = Optic vesicle; *Ot.V.* = Otic vesicle; *T.F.* = Thompson's flexures.

The optic vesicles are large somewhat dorso-ventrally flattened outgrowths which project, one from either side of the anterior part of the fore-brain. They occupy practically the entire lateral walls of the anterior region of the fore-brain, and have not yet begun to be constricted off from the latter. Their cephalic borders pass over directly into the front wall of the fore-brain, whilst caudally each vesicle is marked off from the lateral wall of the same by a crescentic groove. Each vesicle communicates with the fore-brain ventricle by a large opening in front of a crescentic posterior margin.

The ectoderm, which overlies each vesicle, is not thickened, and is separated from the vesicles by a thin sheet of mesenchyme.

The subdivision of the fore-brain into telencephalon and diencephalon is indicated by a slight groove on the dorsal wall of the brain, practically on a level with the hinder borders of the optic vesicles. Corresponding to this groove there is present on the inner surface a slight ridge which runs down on the lateral wall, behind the opening of the optic vesicles. This ridge probably represents the velum transversum.

Below and behind the openings of the optic vesicles, and on the ventral surface of the fore-brain is a well-marked depression, forming the primitive infundibular recess, the projecting floor of which produces a bulging on the roof of the buccal cavity.

The wedge-shaped mid-brain is the shortest of the three divisions and is marked off by two constrictions from the fore and hind-brains, the anterior constriction best marked dorsally, the posterior constriction coinciding with the region of greatest flexure. It shows no evidence of subdivision, as described by Watt, in a younger embryo, and Gage, in an embryo of 29 somites. In this respect it resembles the mid-brain of Johnson's embryo of 24 somites, Thompson's embryo of 23 somites, Van den Broek's embryo of 22 somites and Davis' embryo of 20 somites.

The hind-brain is the largest of the three divisions; it is indeed about one-third of the total length of the whole neural tube. It is connected with the mid-brain by the isthmus and fades gradually into the spinal cord. There is a marked thinning of its roof, but no depression as in Van den Broek's embryo. On its lateral walls six pairs of neuromeres can be seen. They appear in the model of the brain as wedge-shaped bulgings, so arranged that the bases of the 1st, 3rd and 5th, are directed dorsally, and those of the 2nd, 4th and 6th are directed ventrally. The 1st pair has no definite limit in front from the rhombo-mesencephalic groove. The 2nd and 4th pairs of neuromeres correspond with definite down bulgings of the floor of the hind-brain, that related to the 4th pair being more prominent than that of the 2nd pair.

The number of neuromeres recorded in embryos of about the same stage as this is as follows:

Thompson's embryo of	23	somites has	7	neuromeres.
Davis'	20	,,	9	,,
Van den Broek's	22	,,	5	,,

Johnson states that the number of neuromeres in his embryo cannot be ascertained.

Lying in relation with the neuromeres are the following structures: The ganglion of the trigeminus in close relation with the 2nd neuromere, the ganglion of the acoustico-facialis with the 4th neuromere (the acoustico-facialis is the largest ganglion present and can be traced to the 2nd branchial arch), and the ganglion of the glosso-pharyngeus lies in relation with the 6th neuromere. This arrangement agrees with that described by Gage, Johnson, Peter Thompson and Davis, and with Bartelmez, who shows in a table the relation of preotic, otic and postotic primary segments of the hind-brain to the secondary and definitive neuromeres.

The most marked of the neuromeres of this embryo is the 4th or facial which corresponds with the otic neuromere of Bartelmez, and the least distinct is the 6th, which is at a level cranial to the 1st somite.

The ganglion of the vagus is seen in the sections as a small cluster of cells caudal to the ganglion of the glosso-pharyngeus.

The otic vesicle lies in relation with the 5th neuromere and close to the ganglion of the acoustico-facialis. It is a large pear-shaped vesicle, with its long axis in the dorso-ventral direction, its broad end being directed dorsally.

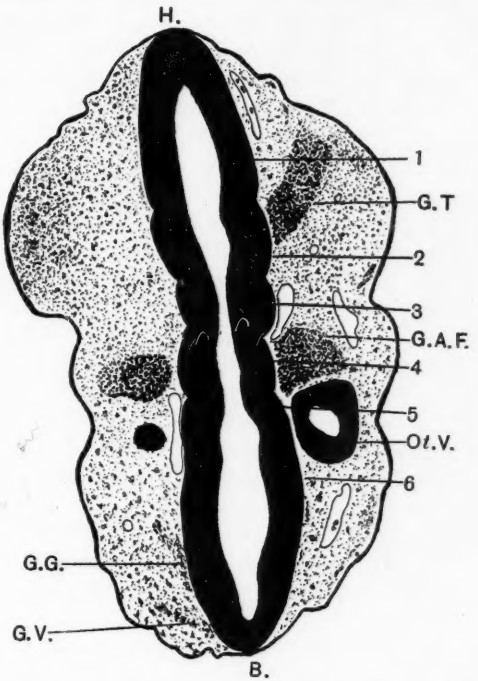


Fig. 3. Camera lucida drawing of Section 23, Hind-brain, showing the Neuromeres and the Ganglia. *B.* = Caudal end; *H.* = Cranial end; *G.A.F.* = Ganglion acoustico-facialis; *G.G.* = Ganglion glossopharyngeus; *G.T.* = Ganglion trigeminus; *G.V.* = Ganglion vagus; *Ot.V.* = Otic vesicle; 1–6 = Neuromeres.

Its wall is thick and the vesicle is still open to the exterior; its opening is situated at its dorsal broader end rather on the lateral aspect than on the summit, and the edges of the opening are continuous with the surrounding ectoderm.

The brain is sharply flexed at the junction of the mid-brain and the isthmus, the mid-brain forming the most cephalic part of the embryo. The longitudinal axes of the fore and mid-brains form approximately a straight line which makes an angle of rather more than 90′ with the longitudinal axis of the cephalic half

of the hind-brain. This flexure corresponds to the primary cephalic flexure in other embryos and involves the anterior end of the notochord. There is a slight flexure of the hind-brain immediately behind the down-bulging related to the 4th pair of neuromeres, and on a level with the otic vesicles.

These two flexures resemble those described by Peter Thompson and Van den Broek in embryos of about the same stage of development as this. Thompson says: "They are so different from those universally regarded as primary cerebral flexures, that one hesitates to go further than simply place them on record." He ends by saying: "Is it not possible that there may be certain flexures of a temporary character, which precede the primary flexures usually described?" Van den Broek expresses a similar view.

Since the publication of Thompson's and Van den Broek's papers, Low, who described Pfannenstiel III embryo of 13–14 somites, finds a similar condition which agrees very closely with that of Thompson's description. Willin also finds a similar flexure in a brain of an embryo of 13 somites, and states: "The brain flexures do not agree with the His models of this stage but correspond more to the older embryos described by Thompson and Van den Broek." Hochstetter also finds a similar condition in an embryo of 3·34 mm., somewhat older than Thompson's. He states: "There is a flexure on the ventral aspect of the hind-brain resembling that described by Thompson though not so marked. This disagrees with the condition described by His." He regards His's embryos, L.G., B.B., E.B., as abnormal or else not well preserved.

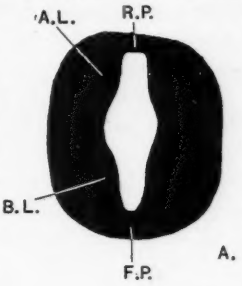
These flexures are probably due to exaggeration of the usual primary flexures. The flexure between the mid-brain and isthmus corresponds very closely with the primary cephalic flexure, and involves the hinder part of the mid-brain. The slight flexure in the hind-brain is probably due to the exaggerated dorsal flexure of the body of the embryo (as seen in Plate I) extending towards the hind-brain and involving its hinder part.

Spinal cord. The spinal cord extends from the caudal end of the hind-brain to the tail. The cephalic part of the tube is of the same character as the caudal portion of the hind-brain, where it is compressed laterally and the long axis of its lumen is dorso-ventral in direction. It becomes more cylindrical caudal to the dorsal flexure. It is segmented through most of its length, the segments being separated from each other by circular constrictions which involve its entire circumference, so resembling the segmentation described by Watt and Johnson, and differing from that of Davis' embryo where they only appear on the lateral surface. These segments are very distinct in the region of the dorsal flexure. Eight distinct segments can be seen in the model in that region. Each neural segment lies between two consecutive somites and opposite each segment the dorsal aorta gives off a dorsal segmental artery. The lateral walls of the tube are thicker than its roof and floor; the roof is thinner than the floor and lies in contact with the dorsal ectoderm.

In cross-section (fig. 4), the lateral walls at the level of the dorsal flexure are differentiated into basal and alar laminae and the lumen of the neural canal

is lozenge-shaped. This differentiation gets less and less marked towards the tail end where the lumen is circular in shape.

Ganglionic crest. The ganglionic crest as a definite wedge-shaped structure is seen in the region between the 8th and 13th somites. In this region it is a continuous band of cells situated in the angle between the spinal cord and the somites near the dorsal middle line, and although it is a continuous mass, it shows signs of segmentation by the presence of constrictions at regular intervals. When traced towards the head end, it thins out and becomes less distinguishable; in some places it is only one cell thick. When it is traced towards the tail end, it again thins out and cannot be seen below the 18th somite.



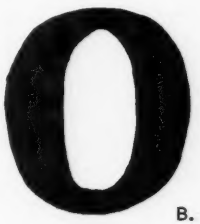


Fig. 4. Cross sections of the Spinal Cord at three levels: *A.* (section 167) at the level of the 10th somite; *B.* (section 218) at the level of the 12th somite; *C.* (section 245) at the level of the 16th somite. *A.L.* = Alar lamina; *B.L.* = Basal lamina; *F.P.* = Floor plate; *R.P.* = Roof plate.

THE DIGESTIVE SYSTEM

Oral cavity. The oral cavity is a transverse slit between the head and the mandibular arches. It is wide transversely and narrow cephalo-caudally. The primitive infundibular recess abuts against its cephalic wall and bulges into its cavity. There is a small recess in the dorsal part of the cavity between its roof and the pharyngeal wall; this recess is the beginning of Rathke's pocket. The bucco-pharyngeal membrane is perforated in two places.

Pharynx. The pharynx (fig. 5) is a large cavity which is flattened dorso-ventrally. Its cephalic limit is the bucco-pharyngeal membrane, but beyond the dorsal limit of the membrane, the cavity extends cranially, forming Seessel's pouch. On each of the lateral walls of the pharynx there are four pharyngeal pouches. The first two are deep long grooves directed dorso-ventrally and inclined towards the head end of the embryo. They are compressed cephalo-caudally, and their lateral walls are in contact with the floors of the first two ectodermal grooves to form the closing membranes, the entoderm and ectoderm of which are not yet fused. The third pouch is very small and its lateral wall does not reach the ectoderm of the 3rd groove. Davis and Johnson find the same condition in their embryos; although three ectodermal grooves are present, only the first two pharyngeal

pouches reach the corresponding grooves. This disagrees with the view expressed by Grosser, who states: "In man the external grooves first become evident when the pharyngeal pouches have come into contact with the ectoderm." The 4th pouch is a very slight dimple on the lateral wall of the pharynx; the ectoderm opposite it is thickened but is not depressed into a groove.

In the roof of the pharynx there is a shallow groove running along the dorsal middle line parallel to the notochord which bends round the cephalic end of the pharynx.

Projecting into the cavity of the pharynx from its ventral wall in the middle line there are two well-marked swellings. The cephalic one is the larger and is situated on a level with the 1st visceral arch (mandibular arch). This knob-like

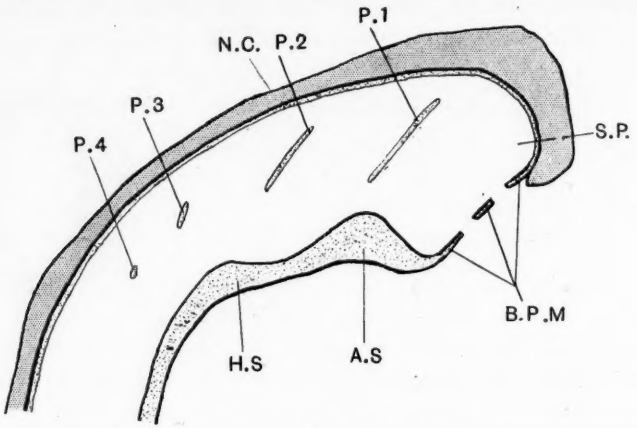


Fig. 5. The Pharynx. *A.S.* = Aortic swelling; *B.P.M.* = Bucco-pharyngeal membrane (perforated); *H.S.* = Heart swelling; *N.C.* = Notochord; *P.* 1. = 1st pharyngeal pouch; *P.* 2. = 2nd pharyngeal pouch; *P.* 3. = 3rd pharyngeal pouch; *P.* 4. = 4th pharyngeal pouch; *S.P.* = Seessel's pouch.

swelling is moulded over the ventral aorta, just before it divides into the 1st pair of aortic arches. The caudal swelling is much smaller and lies dorsal to the atrium. The two swellings are separated from each other by a groove, which is continuous on either side with the 1st pouch. Kingsbury points out that the contour of the ventral wall of the pharynx is influenced by the pericardial area, which lies ventral to it, and there can be little doubt that the two swellings are produced by the parts underlying them, i.e. the ventral aorta underneath the larger causing an "aortic swelling," and the atrium underneath the smaller causing a "heart swelling." Johnson describes two similar swellings, but he follows Grosser in interpreting them as the tuberculum impar and the copula respectively. He also describes a third swelling caudal to the second one and believes it to be the heart swelling. Davis, on the other hand, describes

the same swellings but follows Kingsbury's interpretation of their being due to the influence of the pericardial area. Watt, in his younger twin embryos of 17–19 somites, describes a swelling due to the underlying ventral aorta.

Projecting from the ventral end of the 1st right pharyngeal pouch into its lumen is a villus-like process of cubical epithelial cells with a core of

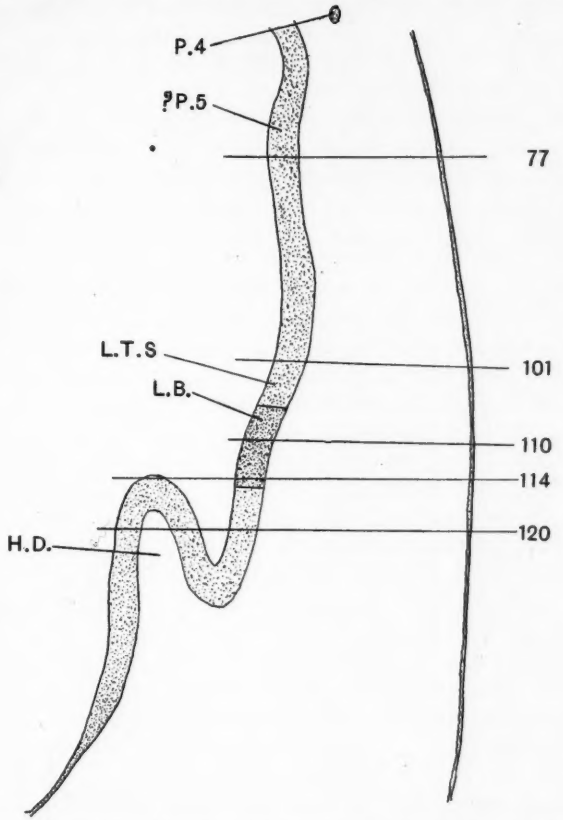


Fig. 6. Left lateral view of the gut between the 4th pharyngeal pouch and the yolk stalk. The numbers on the right denote the cross-sections in fig. 7. *H.D.* = Hepatic diverticulum; *L.B.* = Lung bud; *L.T.S.* = Laryngo-tracheal sulcus; *P.* 4. = 4th pharyngeal pouch; *P.* 5 = ? 5th pharyngeal pouch.

mesenchyme, which is directed dorsally. On the left side a similar process is present but it is shorter and appears as a slight fold of the entoderm of the cephalic wall of the 1st pouch. There is a small cavity in its core which looks very much like a blood vessel. A similar condition has been described by Watt, Davis and Johnson. Grosser also observed the same condition in all young

embryos in which the 1st pharyngeal pouch is well developed. He states: "That it is an accidental structure or due to post-mortem changes seems to be excluded by the regularity of its occurrence. It disappears quite early (in embryos of 4·25, 5·0 and 5·8 mm. and in those still older it is wanting) and may perhaps be interpreted as a rudimentary internal gill."

Caudal to the "heart swelling" which is at the level of the 3rd pouch, the pharynx becomes narrow and its lumen triangular in shape, and its floor bends nearly at right angles. There is no indication of the tuberculum impar or the furcula. The ventral wall of the pharynx is much thicker than the dorsal.

Thyroid. Due to the plane of section which is practically parallel to the floor of the pharynx, the primordium of the thyroid is difficult to determine in this embryo; but there is a definite thickening of the entoderm in the floor of the pharynx between the two swellings, which is the usual position of the thyroid primordium. This thickening of the entoderm extends cranially over the aortic swelling.

Lungs. Caudal to the 4th pharyngeal pouch the fore-gut is prismatic in shape, and its base is directed ventrally. In this area there is a rounded swelling (figs. 6 and 7) which is slightly bifid and is situated a short distance from the 4th pouch. This appears to correspond with a similar swelling in Thompson's embryo. Grosser interprets this swelling as a "questionable fifth pharyngeal pouch."

Dorsal to the sinus venosus and cephalic to the hepatic diverticulum, the fore-gut becomes compressed from side to side, thus forming two lateral walls and ventral and dorsal grooves. As it proceeds caudally the ventral groove becomes deeper and more pointed, and ends in a rounded thickening of the ventral wall. There is a very slight indication of unequal division of the thickened area into a larger right and a smaller left part. The thickened part is the primordium of the lung and the groove is the laryngo-tracheal sulcus.

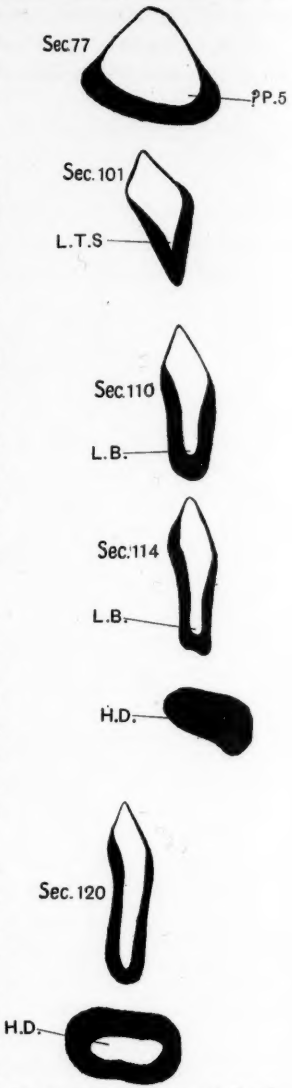


Fig. 7. Cross-sections at the levels marked in fig. 6.

Johnson describes two swellings, one of which corresponds to the bifid,

and the other to the pointed swellings mentioned above, but he was unable to determine their significance from his specimen alone.

Thompson describes somewhat similar conditions and he interprets the bifid one as the lung bud and the caudal one as the beginning of the stomach. Grosser, however, concludes that the first swelling represents probably a 5th pair of pharyngeal pouches and the second swelling, the lung bud.

In Davis' embryo the lung bud has already divided into a large right and a smaller left lobe, a condition older than in this embryo.

Heiss states that the lung area is divided into three parts, two lateral and one median, the latter fusing with the right part. The lung bud in this embryo is in too early a stage to show such a tri-partite condition if it occurs.

The primordium of the lung is very near the hepatic diverticulum, in fact the lung bud and the tip of the hepatic diverticulum can be seen in the same section (fig. 7). This is in accord with the descriptions of Davis and Grosser.

The region between the lung area and the hepatic diverticulum is also compressed laterally and according to Lewis is the gastric region.

Liver. Caudal to the lung bud a large hepatic diverticulum (figs. 6 and 7) is present in the ventral wall of the fore-gut and embedded in the transverse septum. It turns cranially and is directed towards the head end of the embryo where it expands transversely. This expansion is divided into two lateral parts by a shallow vertical groove on its ventral wall. From the walls of the distal part of the diverticulum very short processes sprout out giving its contour an irregular appearance. These are the primordia of the hepatic trabeculae; no further extension of them can be seen. Johnson, describing them in his embryo, states that: "Most of them (trabeculae) are indistinct and their extent is doubtful, for their cells closely resemble those of the mesenchyme and there is no definite line of separation between the two, such as a basement membrane." In this embryo there is no difficulty in seeing these sprout-like processes of the trabeculae, their cells being like those of the diverticulum.

The proximal (attached) end of the hepatic diverticulum is round and has a thick ventral wall. It does not show the irregularity due to the trabeculae seen in the distal part.

The diverticulum seems to be surrounded by blood vessels, and in two or three sections some of these vessels are seen to open into the vitelline veins, which lie on either side of, and dorsal to the diverticulum.

Mid-gut and yolk stalk. A short distance caudal to the hepatic diverticulum the yolk stalk joins the gut; the stalk is a wide short canal. It is compressed laterally and bends to the right and cranially. It opens into the mid-gut, which is also flattened laterally. The ventral wall thins out as it proceeds from the hepatic diverticulum to the yolk stalk. No sign of constriction of the lateral wall of the yolk stalk is seen except the ridge on the right side due to the sharp bend.

Hind-gut and cloaca. Caudal to the yolk stalk the shape of the gut lumen

begins to change; it becomes more or less circular, and as it approaches the cloacal expansion it becomes compressed laterally again.

Near the tail end, the hind-gut is greatly dilated to form the cloaca, the ventral wall of which bulges out and abuts against the ectoderm in the anal pit forming the ano-cloacal membrane. There is no thickening of ectoderm or fusion with the entoderm to be seen in the membrane.

Caudal to the cloaca the hind-gut narrows again for a short distance, forming the end portion of the gut. The gut between the yolk stalk and cloaca is surrounded with a thick layer of mesenchyme, which is rich in blood vessels and blood islands.

Allantois. The entodermal allantois arises as a funnel-shaped tube from the ventral wall of the cephalic end of the cloaca. It is a very narrow canal directed cranially and ventrally to enter the body stalk where it ends blindly. When traced into the body stalk, it runs first between the two umbilical arteries, then it pierces the anastomosis of the two.

THE VASCULAR SYSTEM

Heart. The heart forms a large prominence on the ventral aspect of the embryo, immediately caudal to the head. Its caudal limit is about the level of the middle of the embryo. When the model is viewed from the front, the heart looks like a tilted letter U with the tilt directed from right to left, and from tail to head. The limbs of the U are thick and the space between them is a narrow cleft. They turn dorsally and to the left of the middle line. The right limb is continuous with the ventral aorta, and the left turns sharply dorsalwards to the sinus venosus. The heart lies free in the pericardial cavity except for a small attachment of the dorsal mesocardium to the dorsal surface of the atrium, and the sinus venosus which is embedded in the transverse septum.

The four divisions of the heart, the bulbus cordis, the ventricle, the atrium and the sinus venosus can be seen. The most dependent part of the heart, "the apex," lies to the left of the middle line.

The sinus venosus consists of two lateral horns and an intermediate part. The right horn is larger than the left and communicates freely with the atrium on its dorsal aspect; the opening is marked on the surface by a slight constriction. The sinus forms the most dorsal part of the heart and is embedded in the transverse septum. Each horn receives on its lateral aspect the duct of Cuvier cranially and the vitello-umbilical trunk caudally. The duct is directed dorsally and receives cranially the anterior, and caudally the posterior cardinal vein. The vitello-umbilical trunk, a short wide vein lying in the transverse septum, is formed by the union of the vitelline and umbilical veins. The short intermediate part of the sinus venosus lies transversely in the septum, and a part of it is attached to the dorsal mesocardium. The mesocardium is attached to the dorsum of the sinus venosus and atrium ventrally, and to the dorsal wall of the pericardial cavity dorsally.

There is a short wide vein joining the ventral aspect of the intermediate

part of the sinus, and a similar but smaller one joining the right vitello-umbilical trunk; both are cranial to, and near the hepatic diverticulum. Van den Broek finds a vein similar to the former and thinks "it is possibly connected with the liver."

The atrium is placed dorsal to the bulbus cordis and truncus arteriosus. Its concave ventral surface is separated from them by a transverse narrow cleft. The bulk of the atrium lies on the left side of the ventral middle line and its cranial portion is divided by a notch into two rounded projections, each containing a part of the atrial cavity. The notch corresponds to the attachment of the septum primum internally. The septum is just beginning in this embryo; it arises from the ventral wall of the atrium at the convexity caused by the pushing in of the ventral wall by the bulbus cordis. The septum divides the cranial part of the cavity into two parts as mentioned above. As the atrium joins the ventricle, its cavity narrows, forming the atrial canal, which is indicated on the outer surface by a constriction separating the atrium from the ventricle.

The ventricle begins on the left side from the atrial canal and is first directed caudally and to the right, crossing the ventral middle line after forming the most caudal part of the heart (the apex), then it turns cranially and to the right side, reaching a level slightly caudal to the atrial projections; then it bends ventrally and caudally towards the ventral line to become the bulbus cordis.

The bulbus cordis is well marked and lies between the ventricle and the truncus arteriosus. Its cavity is large at its commencement but narrows near the truncus. On its outer surface it is marked off from the ventricle by a wide shallow groove on its right side; on its left side it is separated by a narrow cleft from the atrium. It forms with the cranial end of the ventricle a V-shaped structure with the open angle directed cranially, with the right limb of the V directed towards the ventricle, and the left limb directed towards the truncus arteriosus (ventral aorta).

According to Keith and Griel, the bulbus cordis is completely incorporated in the right ventricle to form the infundibulum.

The endothelial cardiac tube follows closely the shape of the muscular one. It extends into the projections of the ventricle and the atrium, and is also constricted at the atrial canal. The cavity of the atrium is larger than that of the ventricle, and the opening of the sinus venosus is wide and lies in a transverse direction.

There is a large space between the muscular and the endothelial tubes in the ventricle and bulbus cordis and, to a small extent, in the truncus arteriosus. In the atrium this space exists in the ventral part only, but in the greater part of its wall the two layers are close together. In this respect it agrees with Davis' embryo, but Mall says that the whole muscular wall of the atrium is in contact with the endothelial lining and he states: "This arrangement is so pronounced in the early heart that it affords a way by which we may determine with precision the exact portion of the heart tube from which the atrium arises."

The endothelial tube consists of a single thin syncytial layer; in the space between it and the muscular wall of the heart, the endothelium sends out syncytial processes, some of which are stellate in shape, and others are fork-like. Johnson finds these processes in the bulbus cordis and ventricle, but in this embryo they are also found in the atrium, where the space exists. He says: "The significance of processes of this kind cannot be doubted. They represent the earliest beginnings of the so-called 'heart sinusoids,' which in embryos a little older are numerous. By their growth and anastomoses they give rise to the trabeculae of the heart." It is difficult to imagine the "heart sinusoids" giving rise to trabeculae. Perhaps he means the walls of the "heart sinusoids." The space is also filled with fine, faintly stained fibrils devoid of cells or nuclei forming a meshwork with empty spaces, and here and there are irregular masses faintly stained and devoid of cells. According to Tandler, the space between the two layers is filled up with serous fluid, which appears as clot-like fibrous masses in sections. Johnson described similar masses and fibrils, which, as in this embryo, are due to coagulation of the serous fluid.

Arteries. The arteries comprise the ventral and dorsal aortae, the aortic arches and the umbilical arteries.

The ventral aorta is a very short vessel and soon divides into the 1st pair of aortic arches. It lies in contact with the ventral wall of the pharynx, producing a swelling in it as mentioned before.

There are two pairs of aortic arches; they are directed dorsally and lie cranial to the corresponding pharyngeal pouches. The 1st arch is large and joins the beginning of the dorsal aorta, it is situated in the 1st visceral or mandibular arch. The 2nd arch is much smaller than the 1st and does not join the ventral aorta, and is situated in the 2nd visceral arch. There is a 3rd aortic arch on the right side only, which joins the dorsal aorta and is much smaller than the 2nd and only runs for a short distance in the right 3rd visceral arch.

The 1st arch gives off two branches; one of these arises opposite the fore-brain and represents the internal carotid artery. It runs cranially and joins the plexus at the root of the optic vesicle. The other arises some distance caudally, and joins the plexus round the hind-brain.

The dorsal aorta on either side begins from the dorsal end of the 1st aortic arch and ends behind by breaking up round the end of the gut to form the arterial plexus of the tail. It is not of the same size throughout; it is largest caudally and smallest at the level of the mid-gut.

The dorsal aortae run along the whole length of the embryo, lying close to the notochord and dorsal to the gut. They are at first separated by a wide interval, till they reach the level of the 7th somite, where they approach each other and run as two separate vessels with their medial walls very close together. At the level of the 10th somite, the two vessels begin to fuse together. Davis defines the term "fusion" as "implying the disappearance of the approximated endothelial surfaces, thus establishing a communication between

the lumina of the vessels, and the fusion is termed complete when the opening is of such a size as to obliterate the original bi-tubular condition." Adopting this definition, the two aortae are fused at seven places (fig. 8); the 1st is complete and at the level of the 10th somite; the 2nd, 3rd and 4th are between the 11th and 13th somites, and are incomplete, i.e. the two vessels still retain their shape and the fusion is an hour-glass in shape; the 5th fusion is the largest and lies between the 14th and 16th somites, and is complete. The 6th and 7th fusions are the smallest and lie at the level of the 17th and 18th somites respectively, and appear as if the fusion is just beginning. Caudal to the level of the 18th somite the two dorsal aortae run as separate vessels again.

The dorsal aorta on either side gives off three sets of branches, (*a*) dorsal, (*b*) lateral and (*c*) ventral. These branches are arranged on the whole according to the description given by Evans.

(*a*) There are 15 dorsal segmental arteries on the left and 12 on the right side. According to the table given by Evans, this embryo falls between Graf Spee's embryo (15 somites), which has 11 dorsal segmental arteries and Thompson's embryo (23 somites), which has 21 arteries. Davis' embryo (20 somites) has 14 and Johnson's embryo (24 somites) has 24. Segmental loops are seen in the 1st, 3rd, 4th and 5th branches on the left, and in the 3rd, 5th, 7th and 10th on the right. In these the dorsal branch divides into two branches, i.e. a short median which reaches the lateral wall of the medullary tube and divides into dorsal and ventral branches and a long lateral branch which joins the cardinal vein.

(*b*) The lateral branches are very small, and are seen in the nephric region of this embryo between the 11th and 20th somites, except the 1st artery on the left side, which is at the level of the 6th somite. There are five branches on the left and four on the right. They can be traced laterally towards the nephric system but only in two branches on the left side is it possible to make out a connection between the artery and the loop from the posterior cardinal vein.

(*c*) The ventral branches are not segmental in their arangement, though they arise in pairs. According to

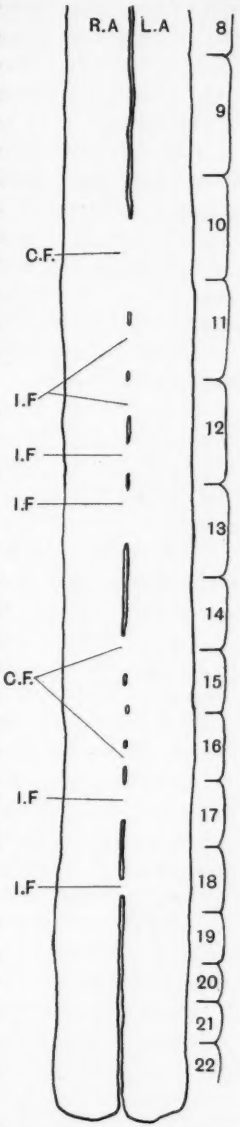


Fig. 8. Fusion of the Dorsal Aortae. *C.F.* = Complete fusion; *I.F.* = Incomplete fusion; 9–22 = Somites.

Evans there is originally a ventral artery for each segment, but those of the more cranial body segments degenerate very early. There are 11 arteries on the left and 10 on the right side. The first two on either side are in the pharyngeal region. The rest are given off in the caudal half of the embryo; three branch off at the level of the yolk stalk and five at the level of the hind-gut.

The umbilical arteries leave the dorsal aorta by two large branches on either side. Very shortly after entering the body stalk they unite so as to enclose the allantoic duct, but they very soon separate again. The right vessel is larger than the left.

The plexus round the brain is distinguishable into three parts. The first is arranged round the fore-brain and is connected with the internal carotid artery and with the beginning of the vena capitis medialis.

The second part of the plexus is arranged round the mid-brain and is the smallest of the three.

The third part is the largest of the three and surrounds the hind-brain. It is connected with an artery arising from the 1st aortic arch at the level of the Vth ganglion. This artery divides into two branches, a cephalic one joining the plexus round the mid-brain, and a caudal branch joining the plexus round the hind-brain.

Veins. They comprise the anterior and posterior cardinal, the vitelline and the umbilical veins.

The anterior cardinal begins from the caudal end of the vena capitis in the region of the hind-brain; as it proceeds caudally it comes to lie near the surface and on the dorso-lateral corner of the pericardial cavity. It joins the posterior cardinal to form the common cardinal vein (duct of Cuvier). It receives a few tributaries, one caudal to the otic vesicle and another from the lateral wall of the hind-brain.

The vena capitis medialis has been traced on the left side. It begins from the plexus round the root of the otic vesicle and runs caudally and close to the lateral wall of the brain, into the anterior cardinal vein. It is freely connected with the plexus round the brain by various capillaries.

The posterior cardinal vein is a discontinuous vessel, which begins at the caudal end of the gut. It proceeds cranially in a position dorso-lateral to the coelomic cavity between it and the somites, and dorsal to the nephric system. It appears in fragments and is connected with the dorsal segmental arteries by the four pairs of loops mentioned above; it is at these connections that the vein is at its best, and this appears to support the view as regard its formation expressed by Evans. He states: "It is probable that lateral loops of the dorsal segmental arteries are instrumental in the formation of these veins, as in the case of the anterior cardinals. This method of formation of the posterior cardinal vein appears fundamental." The vein joins the caudal end of the duct of Cuvier.

The subcardinal veins are seen in the nephric region as disconnected

capillaries, situated ventral to the nephric vesicles between them and the coelomic wall and connected with the lateral segmental branches of the dorsal aorta. Two are seen on the left and one on the right side; the fragments are longest at these connections.

The duct of Cuvier is a short medio-laterally flattened tube; it is situated at the level of the 3rd somite. It receives the anterior and posterior cardinal veins and opens medially into the sinus venosus.

The umbilical veins begin at the chorionic end of the body stalk by the union of several large veins. These first form one vein which then breaks up in the body stalk into a plexus, which re-unites again into the right and left umbilical veins as they leave the body stalk. The left vein is shown in the model. Through its entire course, it lies in the body wall, from which it receives tributaries. At the level of the 5th somite the umbilical vein unites with the vitelline vein to form the vitello-umbilical trunk. This is short and wide, and is situated in the transverse septum and opens into the caudal aspect of the sinus venosus.

The vitelline veins are formed by the plexus round the yolk stalk. They are smaller in cross-section than the umbilical veins, and run on the lateral wall of the mid-gut and enter the transverse septum, where they join the umbilical vein to form the vitello-umbilical trunk.

Blood islands. These are clusters of blood cells varying from one cell to several in diameter. They are distinguished from blood vessels by the entire absence of any sign of vessel wall. They are in contact with the mesenchyme and are chiefly seen in the mesenchyme of the head region, in the mesenchyme surrounding the hind-gut, and in villus-like processes which project from the coelomic wall in the region of the hind-gut.

THE NEPHRIC SYSTEM

The nephric system (fig. 9) consists of pronephros, mesonephros and a primary excretory duct on either side. The pronephros is more in the form of vesicles than tubules and the mesonephros is in the form of a segmented cord.

The arrangement differs slightly on the two sides. On the right side there are six pronephric vesicles; the 1st is at a level between the 8th and 9th somites. The cranial three-quarter of the 2nd vesicle lies at the level of the 10th somite. The caudal quarter of the 2nd, the whole 3rd and the cranial half of the 4th vesicle lie at the level of the 11th somite. The caudal half of the 4th, the whole of the 5th, and cranial half of the 6th lie at the level of the 12th somite. The caudal half of the 6th lies at the level of the 13th somite. Each of the six vesicles has a lumen, and each is connected with the coelomic wall by a solid strand of cells. This connection is thicker in some than in others. In none of these strands (which represent remains of the nephrostomes) is a lumen seen. There is a gap between the 1st and 2nd vesicles of about $1\frac{1}{2}$ somites.

Caudal to the last vesicle, the mesonephros appears as a cord running to the end of the embryo, where it ends in the coelomic wall near the undifferentiated

mesodermic mass of the tail. It has an interrupted lumen, and its cranial part is segmented, showing three segments separated by three constrictions, and there is a lumen in each of these segments. The mesonephros is also connected with the wall of the coelomic cavity by the remains of the nephrostomes.

The primary excretory duct begins with the 2nd pronephric tubule and ends in contact with the ectoderm at the level of the last somite. It is interrupted between the 2nd and 3rd pronephric vesicles, but from the 3rd to its end it runs as a continuous duct. It has an interrupted lumen but this does not communicate with the lumen of the pronephros; its connection is only by its wall. The duct is entirely separated from the mesonephros and is situated very close to the ectoderm.

On the left side there are also six pronephric vesicles but they differ in their arrangement from the right side. The 1st, 2nd and cranial half of the 3rd are at the level of the 11th somite. The caudal half of the 3rd, the whole of the 4th and cranial half of the 5th vesicles are at the level of the 12th somite. The caudal half of the 5th and the whole of the 6th vesicles are at the level of the 13th somite.

With the exception of the 1st vesicle, they all possess a lumen. The mesonephros and the primary excretory duct are like those on the right side, except that there appear to be six mesonephric segments instead of three, and the duct is interrupted between the 4th and 5th vesicles, instead of between the 2nd and 3rd on the right side.

The above description differs in one important respect from that given by Felix, and that is the asymmetry and

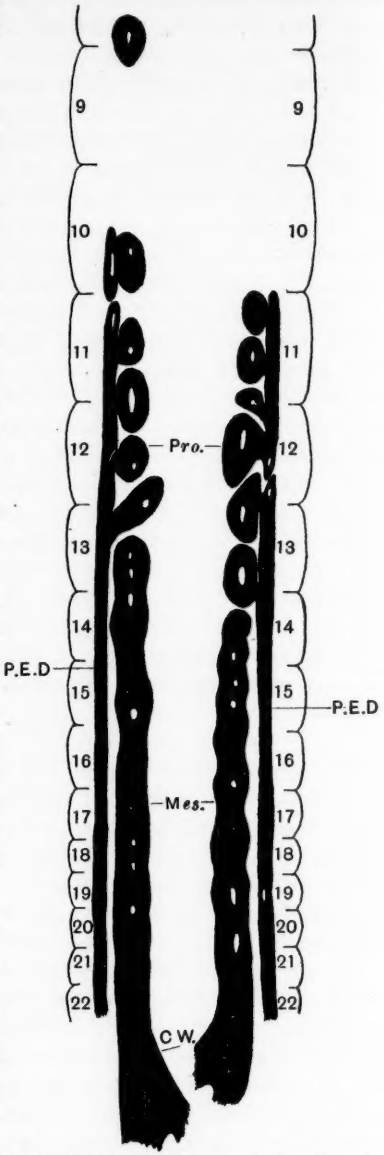


Fig. 9. The Nephric System. *C.W.* = Coelomic wall; *Ect.* = Ectoderm; *Mes.* = Mesonephros; *P.E.D.* = Primary excretory duct; *Pro.* = Pronephros; 9–22. = Somites.

entire absence of metameric arrangement in the pronephric vesicles of the two sides. According to Felix the pronephric duct is formed by the union of the caudal ends of the pronephric tubules, and its subsequent growth caudally. In this embryo the duct has almost become an independent structure, the connection of the pronephric vesicles with the duct being none too complete and in some being only one cell thick.

Johnson and Watt found the same condition as described by Felix, though Johnson found that the mesonephros in his embryo is a cord-like structure with irregular swellings (the mesonephric vesicles), a condition similar to that of this embryo.

SOMITES

There are 22 pairs of somites extending from the caudal part of the hind-brain to the level of the posterior neuropore. The first pair of somites is in the region of the caudal part of the hind-brain. The somites are in different stages of development, more advanced towards the head and less so towards the tail end.

The last pair (22nd) is a solid mass just separating from the tail mass. The 21st, 20th, 19th, 18th and 17th pairs are cubical in shape, with dorsal, lateral, ventral and medial walls composed of epithelial cells about four layers thick and surrounding an empty myocoelic cavity. From the 16th to the 11th pair, they become compressed and more or less oval in shape and their walls are arranged in two laminae, i.e. a lateral or dermatome and a medial. The latter divides into two parts, a dorsal (myotome), whose cells are epithelial in character, and a ventral (sclerotome), the cells of which are mesenchymatous in appearance. The myocoele is still free from cells but in the 10th and 9th pairs it becomes invaded by cells from the sclerotome. From the 8th to the 4th pair, the sclerotome attains a large size and is wedge-shaped in cross-section. Its apex is directed to the angle between the medullary tube and the notochord, and its base is separated from the dermatome by a slit-like space. The myotome is short and its dorsal end joins the corresponding end of the dermatome. The 3rd, 2nd and 1st pairs are not sharply separated from each other. Each consists of two laminae whose cells are epithelial in character. On cross-section these somites are triangular in shape; the apex is directed dorsally and the base is ill-defined and fuses with the adjacent mesenchyme.

NOTOCHORD

The notochord begins caudal to the primitive infundibular recess and ends in the undifferentiated mesodermic mass of the tail. Its tapering cephalic extremity is situated immediately behind the attachment of the bucco-pharyngeal membrane and fuses with the entoderm of the roof of the pharynx for a short distance from that attachment; as it extends caudally from this region it is separated from, but lies close to the roof of the pharynx. It gradually becomes close to the ventral surface of the medullary tube, a position it retains

to its caudal end. Cranially, the notochord is sharply bent over the cephalic end of the pharynx, and there is a distinct swelling in the bent part which fits in the flexure between the mid-brain and isthmus (primary cephalic flexure).

In cross-section the notochord is cylindrical in shape, except at its cephalic end, where it is slightly laterally compressed.

It is invested completely on its lateral sides by mesenchyme; ventrally it is also surrounded by mesenchyme except where it is close to the roof of the pharynx. Dorsally it is surrounded by mesenchyme up to the level of the 7th somite. Caudally to this, the notochord is very closely applied to the ventral surface of the medullary tube. This agrees with the condition found by Johnson and others.

As the notochord is closely applied to the ventral surface of the medullary tube from the 7th somite backwards, it follows the segmental constrictions and expansions of the tube, thus forming segmental flexures.

The cells forming the notochord are wedge-shaped; their nuclei lie towards the periphery. In some sections a lumen is seen. The notochord is surrounded by a delicate membrane as described by Van den Broek.

TRANSVERSE SEPTUM AND COELOM

The transverse septum is a thick plate of mesenchyme with a mesothelial covering. It is placed in an oblique plane, starting from the ventral body wall caudal and ventral to the heart and at the level of the 8th somite. It passes obliquely, dorsally and cranially to the level of the 4th somite; its obliquity thus occupies a length of four somites. This corresponds to the position and obliquity of the septum of an embryo between the 2 mm. and 4 mm. embryos in Mall's scheme of the position of the septum of embryos between 2 mm. and 24 mm. long, but Thompson, Davis, Johnson and Watt place the septum in their respective embryos at a more cranial level than it occupies in this embryo. Its dorso-cranial border is crescentic in shape with the cornua attached to the lateral body wall. In the middle it is attached to the dorsal mesocardium, and on either side of this attachment the border is free, so that there is left an aperture of communication between the pericardial and pleuro-peritoneal cavities, and its mesothelial covering is continuous with that of the dorsal mesocardium. The fore-gut invades it dorsally, and in it the hepatic diverticulum is embedded. The part containing the gut and the diverticulum is much thickened, and the thickening bulges into the pericardial cavity, causing a concave impression on the dorsum of the heart, and fills up the space between it and the fore-gut. In cross-section the thickening is pear-shaped with the broad end on the left side where the heart is farthest from the gut. At its caudal end the vitello-umbilical trunk on either side enters the septum to reach the sinus venosus, which lies across it. At its cephalic free border, the duct of Cuvier is carried medially to the sinus venosus through the cornu on either side. No sign of Mall's pulmonary ridge is yet seen.

The pericardial cavity. The transverse septum divides the body cavity transversly into two unequal divisions; the cephalic division (pericardial cavity) is the smaller. It is a single cavity except for a short distance where it is divided dorsally by the dorsal mesocardium in the middle dorsal line. Its cranial limit is at the bulbus cordis and it is bounded dorsally by the pharynx and transverse septum, and ventrally and laterally by the thin body wall. Its floor is formed by the transverse septum which is deficient dorso-laterally where the cavity communicates freely with the pleuro-peritoneal cavity.

The pleuro-peritoneal cavity. It begins at the level of the 5th somite and for some distance it lies dorsal to the pericardial cavity. It is divided by the gut into two lateral divisions, i.e. the pleuro-peritoneal passages. The cephalic extremity of each division communicates with the pericardial cavity; cranial to the yolk stalk where the amnion is reflected from the caudal end of the pericardium, the two divisions communicate transversely and ventral to the gut. At the level of the attachment of the yolk stalk with the mid-gut and for some distance cranially and caudally to that level the two divisions communicate with the extraembryonic cavity. At the region of the hind-gut the two divisions join ventral to the gut. Just in front of the level of the cloaca the two divisions of the pleuro-peritoneal cavity separate again where the umbilical vessels and allantois leave and enter the embryo. They remain separated up to their caudal termination so that in this region there is a ventral mesentery as well as a dorsal one.

THE AMNION

The amnion forms a closed sac in which the embryo lies; it is formed by two layers of flattened epithelium with a thin layer of mesenchyme between them. The inner layer is continuous with the ectodermal integument of the embryo and the outer layer is continuous with the mesodermal lining of the body cavity.

The line of attachment of the amnion to the embryo is as follows: cranially the amnion is reflected from the caudal border of the ventral wall of the pericardial cavity, so that the whole heart, head and the region of the embryo cranial to the apex of the heart lie freely in the amniotic cavity. From the pericardial reflection the amnion sweeps round caudally and is reflected from the ventral border of the lateral body wall and proceeds to the body stalk. At the region of the stalk the two lateral lines of reflection begin to converge, leaving the body of the embryo and proceeding on the surface of the body stalk that faces the embryo. There they meet, forming a V-shaped attachment with the angle of the V directed towards the chorionic end of the body stalk. It will be seen that the line of reflection of the amnion is an elliptical opening on the ventral aspect of the embryo; through this opening the yolk stalk and body stalk emerge. The line of demarcation between the amnion and the lateral wall of the embryo is very marked, due to the sudden thickening of the body wall.

SUMMARY

Dimensions. Chorionic vesicle, 18 × 13 mm. Embryo, 2·9 mm.

Age. About 30 days.

External Form. Head is slightly flattened and flexed. Cervical and caudal flexures. Ventral flexure caudal to yolk stalk. Longitudinal twist; head to the right and tail to the left.

Somites. 22. The last pair is still attached to the tail mass.

Notochord. The thickened cranial end is bent and fused to the cephalic wall of the pharynx. Caudal end terminates in the tail mass. It is surrounded by a delicate membrane.

Nervous System. Two flexures (Thompson's flexures) in the brain, one at the junction of the mid-brain and the isthmus, and the other in the hind-brain. The three main divisions of the brain (fore, mid, and hind-brains) are present.

Fore-brain. Optic vesicles are separated from the ectoderm; no lens primordium. Primitive infundibular recess present. Slight indication of sub-division into telencephalon and diencephalon.

Mid-brain. Shortest division.

Hind-brain. Thinning of the roof. Six neuromeres. Ganglia of V, VII, VIII, IX and X. Otic vesicle still open to the exterior.

Spinal Cord. Segmented for the most part.

Ganglionic Crest. Present between 8th and 13th somites.

Digestive System. *Oral Cavity.* Oral plate perforated in two places. Beginning of Rathke's pouch.

Pharynx. Four pharyngeal pouches; the first two reach the ectoderm. The ectoderm is thickened opposite the other two. Two swellings in the floor of the pharynx, the cranial one the larger and due to the ventral aorta, the caudal one small and due to the pericardium. Two processes ("internal gills" of Grosser) are seen in the 1st pair of pouches, one in each pouch.

Thyroid. There is a thickening of the entoderm between the two swellings in the floor of the pharynx.

Lung. Laryngo-tracheal sulcus and bifid bud lung are present caudal to the 4th pharyngeal pouch.

Liver. A large hepatic diverticulum and trabeculae lie caudal and close to the lung bud.

Yolk Stalk. Is very wide.

Cloacal Membrane and *Anal pit* are present.

Vascular System. *Heart.* S-shaped stage. Four divisions well marked. Sinus venosus, atrium, ventricle and bulbus cordis. The latter is well marked. A large venous cavity appears on the ventral aspect of the sinus venosus. The sinus has two horns and an intermediate part. Each horn receives the duct of Cuvier and the vitello-umbilical trunk. Atrium shows the beginning of the

septum primum. The endothelial cardiac tube follows the shape of the myocardial heart, and is separated from it by a space, except in the greater part of the atrium where it is in contact. The space contains coagulated serous fluid and cardiac trabeculae.

Aortic Arches are two on either side; the 2nd is incomplete. A 3rd is just beginning on the right side.

Dorsal Aortae fuse between the 10th and 18th somites. Dorsal segmental branches are 15 on the left and 12 on the right side. Ventral branches are 11 on the left and 10 on the right side. Lateral branches are 6 on the left and 2 on the right side.

Umbilical arteries unite at the beginning of the body stalk. Each joins the aorta of the corresponding side by two branches. The right is larger than the left.

Veins. Complete anterior and incomplete posterior cardinals. Beginning of the subcardinal. Umbilical vein is larger than the vitelline.

Nephric System. Six pronephric vesicles are present on either side. Each has a lumen except the 1st left. Mesonephros is a segmented cord and ends in the coelomic wall at the tail end. Primary excretory duct interrupted once on either side, and ends in the ectoderm at the level of the last somite. Connected by its wall only to the pronephric vesicles.

Transverse Septum. Crescentic in shape; the middle part is much thickened. It lies obliquely between the 4th and 8th somites. Its dorsal border is attached to the dorsal body wall by the cornua and middle part of the crescent only, leaving two openings on either side of the middle line, through which the pericardial and the pleuro-peritoneal cavities communicate.

CONCLUSION

This embryo falls into a group of embryos of about the same stage of development whose descriptions have already been published.

Peter Thompson (1907) described Robert Meyer's embryo 300 of 23 somites. Van den Broek (1911) published an account of two embryos of 22–23 somites. Bujard (1915) gave an account of Eternod-Delaf's embryo of 20 somites, which he regarded as pathological. Johnson (1917) described an embryo of 24 somites, and Davis (1923) described an embryo of 20 somites. All these embryos very closely resemble the one described in this paper, and on the whole my observations confirm those made by the above-named authors, though there are certain points of difference.

The flexures of the brain in this embryo agree with those first described by Thompson in 1907, and later by different authors. Van den Broek found "Thompson's flexures" (as I venture to call them) in his 22-somite embryo. Low, in 1908, described Pfannenstiel's embryo III of 13–14 somites and he states: "The brain flexures do not agree with the His models of this stage, but correspond more to the older embryos described by Thompson and Van den

Broek." In 1913 Willin reported an embryo of 13 somites with "Thompson's flexures."

In 1919 Hochestetter described a somewhat older embryo than Thompson's, and found similar flexures though less marked. He regarded His's embryo L.G., B.B., E.B., as abnormal or else not well preserved.

Thompson's view was that these two flexures are special flexures of a temporary character which precede the definitive ones. That may hold good for the more caudal of the two but the more cephalic appears to be none other than the usual primary cephalic flexure. The small size of the mid-brain and the narrowness of the fore-brain found in this embryo, and observed also in the figures of the brains of the embryos described by Thompson, Van den Broek and Hochstetter would appear to be features characteristic of the early human brain.

In the nephric system the pronephric tubules are in the form of vesicles, and the primary excretory duct is well formed, with one interruption only. This appears to be an older stage than that described by Felix, Johnson and Watt in embryos more or less of the same age as this. There is also another difference in the nephric system of this embryo from others and this is the entire absence of metamerism in the system.

While reviewing the literature on the subject I noticed the chief criteria used for classifying early embryos are length and age. When comparing embryos of the same length or nearly so, a great difference is found in the stage of their development. For example, Broman's embryo measured 3 mm. and has 35 somites, limb buds and other characteristics much older than Watt's embryo of 3·37 mm. and Bremer's embryo of 4 mm. Waterson described an embryo measuring 2·9 mm. with 27 somites, and possessing other characteristics older than the 2·9 mm. embryo described in this paper. Many other examples can be quoted to show the fallacy of the length of embryos as a criterion for classification. There are many factors which influence the length of an early embryo, i.e. the different degrees of shrinkage and flexures in different embryos, the different methods of measuring used by different observers and possibly also the normal variations between embryos such as are found between adults. As regards the determination of the age of embryos, if we could know the fertilisation age that would be the best and most decisive criterion, but the fertilisation age will be always a hypothetical one worked out by varying data by different authors, and the margin of error, though it may be counted in a very few days, or even hours, makes a great deal of difference in the stage of development reached. Embryos in their early life grow very rapidly and a few days—nay—a few hours may transfer an embryo from one stage to another.

Davis advocates the closure of the neuropores as a reliable criterion. He says: "The closure of the neuropore is perhaps the best criterion we possess for the classification of this particular stage of embryonic development." The variation in the closure of the neuropore has been pointed out in this paper

(p. 386), though it is not so frequent and marked as are variations in length and age. I find the number of somites is the best criterion we possess up to the present, especially as the somites appear very early and are easily demonstrated.

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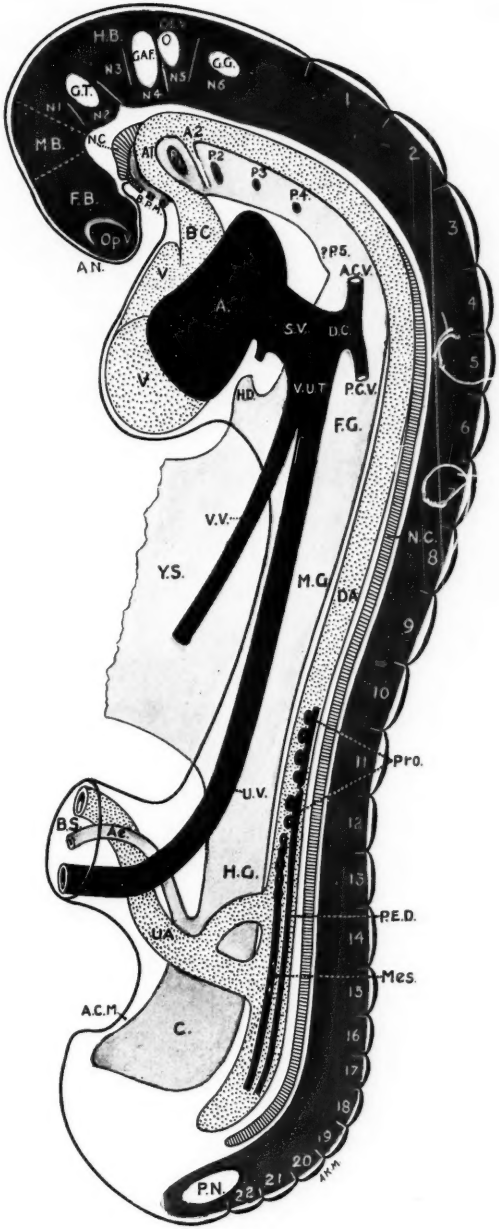
DESCRIPTION OF PLATE

A. = Atrium; *A* 1, *A* 2 = Aortic arches; *A.C.M.* = Ano-cloacal membrane; *A.C.V.* = Anterior cardinal vein; *Al.* = Allantois; *A.N.* = Anterior neuropore; *B.C.* = Bulbus cordis; *B.P.M.* = Bucco-pharyngeal membrane; *B.S.* = Body stalk; *D.A.* = Dorsal aorta; *D.C.* = Duct of Cuvier; *F.B.* = Fore-brain; *F.G.* = Fore-gut; *G.A.F.* = Ganglion acoustic-facialis; *G.G.* = Ganglion glosso-pharyngeus; *G.T.* = Ganglion trigeminus; *H.B.* = Hind-brain; *H.D.* = Hepatic diverticulum; *H.G.* = Hind-gut; *M.B.* = Mid-brain; *Mes.* = Mesonephric cord; *M.G.* = Mid-gut; *N* 1–*N* 6. = Neuromeres; *N.C.* = Notochord; *Op.V.* = Optic vesicle; *Ot.V.* = *Otic* vesicle; *P* 1–*P* 5 = Pharyngeal pouches; *P.C.V.* = Posterior cardinal vein; *P.E.D.* = Primary excretory duct; *P.N.* = Posterior neuropore; *Pro.* = Pronephric vesicles; *S.V.* = Sinus venosus; *U.A.* = Umbilical artery; *U.V.* = Umbilical vein; *V.* = Ventricle; *V.U.T.* = Vitello-umbilical trunk; *V.V.* = Vitelline vein; *Y.S.* = Yolk stalk; 1–22 = Somites.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THE FRENULA VALVULAE COLI

By A. H. RUTHERFORD, M.D. (Edin.)
Sydney, Australia

In order to study the nature of the Frenula Valvulae Coli several specimens were obtained within twenty-four hours after death and placed in 10 per cent. formalin. These specimens were obtained by cutting the ascending colon transversely across, above the ileo-caecal valve and the frenula. The caput caecum coli was then inverted in order to show the ileo-caecal valve and frenula. Two of these specimens are shown in figs. 1, 2. If we consider these specimens, we shall see that the bands of the frenula, starting from the ileo-caecal valve on each side, are continued round the gut forming a more or less deep band of tissue, projecting from the bowel wall nearly 1 cm. and about the same, roughly, across the base. If this projection is taken in the fingers, it feels like a piece of rope. The appearance of the frenula in the human subject is not observable till some hours after death.

In my description of this muscular band, or sphincter, which projects into the lumen of the large intestine at the junction of the caecum and colon, I suppose the caecum to be placed in the position it occupies during life. The caeco-colic sphincter is then seen as a projection of muscular tissue running round the bowel from either side of the ileo-caecal valve. The width and height (vertical to the surface of the bowel) of this sphincter in the specimens examined varied in the development of the muscular fibre and in the degree of contraction in these fibres caused by the 10 per cent. formalin solution. The average was about 1 cm. broad by 1 cm. in height. The anterior longitudinal band of the large intestine is now to the front (anterior) and the posterior longitudinal band to the back (posterior) of the specimen. In this position, taking the ileo-caecal valve, which lies between the two longitudinal bands, as the point of the caeco-colic sphincter, we find that there are two parts of the sphincter—one part passes from the right of the ileo-caecal valve round the anterior mucous surface of the bowel for about 5 cm. to a point on the interior of the bowel corresponding to the anterior longitudinal band on the peritoneal surface. At this point the muscular band becomes aponeurotic—the aponeurotic fibres blending with the anterior longitudinal band. The frenulum, or caeco-colic sphincter, passing from the left and posterior border of the ileo-caecal valve, runs backward round the interior of the bowel for about 9 cm. It circles round the bowel to the front to join the anterior longitudinal band, about $1\frac{1}{2}$ cm. above the shorter band which runs to the right on the opposite side of the ileo-caecal valve to join the anterior longitudinal band. Where the muscular band, or sphincter, passes over the posterior longitudinal band, on its way

towards the anterior longitudinal band, it is seen to be connected with this band by aponeurotic fibres. The muscular sphincter is much more distinct in the fresh specimens because the delicate tissues contain more fluid. The aponeurotic connections to the longitudinal bands are not well seen until the specimens are placed in methylated spirit, which reduces the fluid in the tissues.

In the case observed, by the writer, in 1905, mentioned in his book *The Ileocaecal Valve* (Lewis, London, 1914), where the ileo-caecal valve and caecum were seen through an artificial anus, frenula were not in evidence during life. In the microscopical section (Plate B, and Diagram II) muscular fibres (*M.F.*) of the frenula are shown. There are certain factors that help to account for frenula not being observed during life. One is that the mucous membrane is much thicker in the living subject than it is after death because of the fluids contained in it during life, which tend to conceal the structure of the frenula. Since their fluids are drained off after death and as a result of post-mortem rigidity, the muscular fibres of the frenula become more evident after death. Also, the effect of formalin must be taken into account, causing the contraction of the muscular tissue after death, and rendering the bands of the frenula more distinct.

In the specimens, however, shown in my book (Photographs 8 and 13) which were preserved in formalin, a well-marked ring of contraction is seen running from one side of the ileo-caecal valve round the bowel to the other side of the ileo-caecal valve.

Microscopical Sections. Taking three specimens prepared by placing them in 10 per cent. formalin, microscopical sections were made, cutting vertical to this band at different distances round the bowel, in order to study the tissue composing the band. Two specimens were taken, Nos. I, and II. From No. I sections were taken at the points marked A, B, E, and G. From the specimen No. II sections were taken at the points marked C, D and F. These sections have a similarity to each other. We find that the projection into the bowel lumen, and running round the bowel from one side of the ileo-caecal valve to the other, is made up almost entirely of muscular tissue, with an increase of aponeurotic tissue in the regions corresponding to the position of the longitudinal bands on the peritoneal surface. The mucous membrane covering the caeco-colic sphincter is that common to the large intestine. The arrangement of the muscular fibres in all the microscopical specimens examined is the same. In each side of the projection, or band, the circular coat of the large intestine enters that of the colon on one side and that of the caput caecum coli on the other. The one coat is continuous with the other at the summit of the band. Between the two layers run the longitudinal fibres continuous with the longitudinal coats of the bowel on each side of the band. The arrangement resembles a folding of the large bowel in its circumference at each side of the ileo-caecal valve, which folding has become fixed in this position but excluding the peritoneum from the fold, the apex of the fold projecting into the lumen of the

bowel. The exact angle of the direction of the medial axis of the sphincter to the long axis of the bowel in these specimens was probably modified by the artificial inversion of the caecum. In some cases in which the muscular fibres were tonically contracted, the projection was compact with a rounded summit, as it appeared in section H. In others the projection was longer and thinner, and in one it was bent on its long axis, almost at a right angle. Under the microscope the sections from a portion of the tissue just mentioned which had been straightened out in the paraffin before cutting were examined. The microscopical sections showed the same arrangement of the muscular tissue elements, but the fibres were elongated as if they were semi-relaxed. The result of this arrangement of the vertical unfolding of the muscular coats of the large intestine is that there is a well-marked sphincter at the region of the junction of the caecum and ascending colon.

Professor T. B. Johnston, *Journal of Anatomy*, vol. LIV, 1919, pp. 66–78, deals with the ileo-caecal region of *Callicebus personatus*. In this article he describes the caeco-colic sphincter at the junction of the caecum and colon, on either side of the ileo-caecal valve. He shows, p. 69, a microscopical section of this sphincter. From Professor Johnston's description, and the photograph of the section, shown p. 69, it will be seen how closely the details correspond to those put forward in this article on the human being.

Function. There is, as may be seen by the previous description, a sphincter running transversely round the bowel at the junction of the caecum and the ascending colon, starting from the ileo-caecal valve on the one side, and passing round the ileo-caecal valve on the other.

What is the function of this sphincter? It is a fact known to clinicians, that heavy metallic substances taken by the mouth, or, as in the case of a Murphy's button, introduced into the bowel wall, are successfully passed *per anum* unless too large. The writer remembers a boy of six swallowing a penny and passing it *per anum* without difficulty. If the musculature of the caput caecum coli were passive, heavy articles would tend to come to rest as in a plumber's V-trap. The action of the sphincter at this position appears to the writer to be twofold. By its contraction to form a narrow opening through which the contents of the caput caecum coli can be ejected into the colon, and, secondly, by its further contraction to close the lumen of the bowel and prevent digested food and heavy bodies passing back into the caput caecum coli, the contraction can be maintained until the former contents of the caput caecum coli are under control of the muscular walls of the colon.

Considering the question of digestion in the caput caecum coli, the caeco-colic sphincter would, when contracted, hold the contents in the caput caecum coli until digested. From the specimens examined, it would appear that the naked-eye appearance and microscopical sections of the sphincter vary in different specimens, not only in the development of the muscular tissue, but also in the degree of its contraction, under the action of formalin. The appearance of the microscopic section varies largely according to the

angle at which the section has been cut. It would appear to the writer that the caeco-colic sphincter is functionally active in the human being.

Professor A. Keith ("Anatomical evidence as to the Nature of Caecum and Appendix," *B.M.J.* 1912, vol. II, p. 1601) states that

> The same three divisions are to be recognised in the human ileo-caecal region, caecal colon, caecum and appendix. (See fig. 1.)...In the human caecum this sphincter ring (caecal sphincter) is permanently united with the ileo-caecal orifice, and forms the well-marked retinacular bands....As yet we know nothing of the action of the retinacular of the human caecum, but from what we know of their action in other animals we may safely infer that during caecal digestion they can regulate the passage of the colic and iliac contents to and from the caecum.

Keith brings forward no descriptive or microscopical evidence to support his views[1]. Keith also describes a caeco-colic sphincteric tract in the human subject, which the writer has been unable to demonstrate. In his statement that the human caecum is not in a state of retrogression, though having no knowledge of a sphincter higher up the colon, as described by Professor A. Keith, which acts as the sphincter of the caecum, the writer supports his (Keith's) views that the human caecum is not in a state of retrogression.

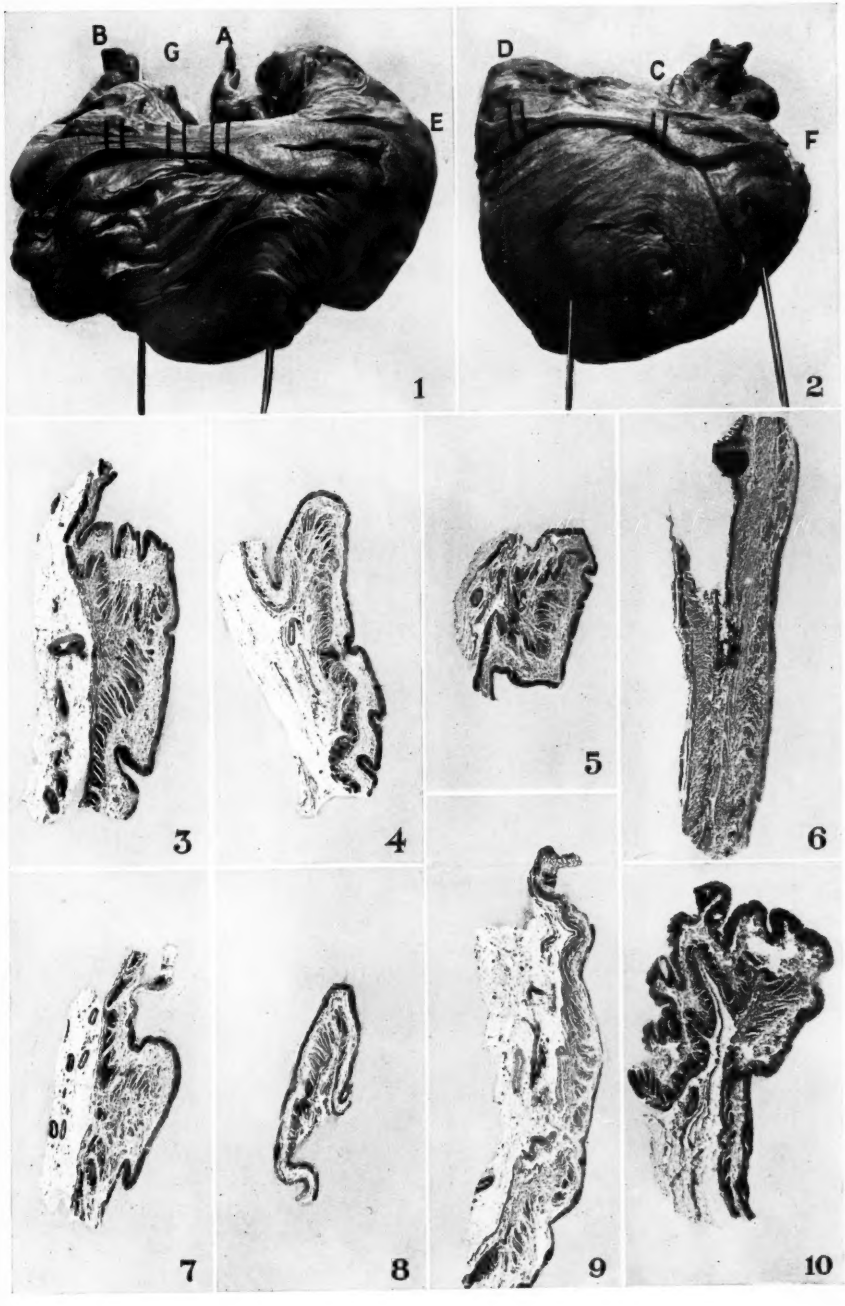
This view is contrary to conclusion 4 put forward by T. B. Johnston. The reason of the doubt expressed by Professor Johnston in the fourth conclusion, i.e. "The human caecum which possesses no competent caeco-colic or intra-colic valve is in a state of retrogression" is, in the writer's opinion, probably because the tissues of the human subjects examined by Professor Johnston are those as seen in the anatomy rooms, which are not suitable for examination of the finer tissues—the tissues being too relaxed and putrefaction having set in.

In several caeca obtained from post-mortem specimens the muscular tissue reacted quite differently, one from another, on being placed in 10 per cent. formalin. The muscular contraction caused by the formalin seemed to depend on the "vitality" still remaining in the tissues. Whereas the examination of the caeca in monkeys would be carried out immediately after death, that on the human subject must necessarily be some hours after death. In the dissecting rooms the examination would not take place for some days, when the muscular tissues of the bowel being so delicate the caeco-colic sphincter would be indistinguishable from the rest of the bowel wall. In the same way the ileo-caecal valve, unless examined soon after death, relaxes and its muscular tissue cannot be distinguished.

CONCLUSION

1. That the human frenula are in reality the caeco-colic sphincter in the human subject.
2. That the human caeco-colic sphincter is functionally active.

[1] Microscopic evidence is given in Keith's original paper. See *Journ. Anat.* vol. XXXVIII (1904), p. vii. (Editorial note.)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DESCRIPTION OF PLATE

Fig. 1. Caecum everted and hardened to show frenula. The sites of the various sections are shown. (Specimen I.)
Fig. 2. Caecum everted and hardened to show frenula. The sites of sections are shown. (Specimen II.)
Fig. 3. Section at *A*, specimen I.
Fig. 4. Section at *B*, specimen I.
Fig. 5. Section at *G*, specimen I.
Fig. 6. Section at *E*, specimen I.
Fig. 7. Section at *C*, specimen II.
Fig. 8. Section at *D*, specimen II.
Fig. 9. Section at *F*, specimen II.
Fig. 10. Section of another specimen taken at the site marked *A*, fig. 1.

A RARE ABNORMALITY OF THE OCCIPITAL BONE

By C. F. T. EAST, M.A., B.M., M.R.C.P.

THE following is the description of a rare abnormality of the occipital bone found at the autopsy of an infant aged four months.

Clinical History. The infant, a boy suffering from hydrocephalus, when he was four weeks old, was admitted into King's College Hospital under Dr Still. The enlargement of the head was first noticed when he was a fortnight old. The head was typically hydrocephalic, its maximum circumference being 18½ inches. The arms and legs were spastic and both optic discs were atrophic. The Wassermann reaction was negative and the cerebro-spinal fluid normal. A decalcified bone tube was inserted into the lateral ventricle on the right side. The treatment, however, was of no avail and the child gradually wasted and died.

Autopsy. The cranium showed the usual appearances of hydrocephalus. The decalcified bone tube was found to be blocked by lymph. The cerebral cortex was about 3 mm. thick. The lateral ventricles contained about a pint and a half of fluid. The foramina of Monro were not obstructed and the choroid plexus was normal. There was no basal meningitis. On stripping off the dura mater an abnormal bony formation surrounding the foramen magnum was found.

The occipital bone exhibits the following remarkable features. On its upper or endocranial aspect are two very prominent ridges which form the lateral boundaries of the foramen magnum (fig. 1). The two ridges end in front in thickened prominences which border the jugular foramina (fig. 1, *d*); they converge behind and terminate on either side of the hinder margin of the foramen magnum in processes which stand up about 3 mm. above the general surface of the bone, there being a median interval of about 4 mm. intervening between the two processes (fig. 1, *b*).

Behind the foramen magnum is an abnormally wide and relatively deep vermian fossa (fig. 1, *a*) which is bounded on either side by curved ridges.

The upper surface of the basilar part of the occipital bone (basilar groove) is deeply concave.

The lateral parts of the occipital bone are very thin and rather deeply concave. The left anterior condylar foramen is partly divided into two by spicules of bone. The under surface of the bone is normal. The superior and posterior semicircular canals stand out very prominently. The cervical vertebrae are normal.

Comment. The abnormal features of the occipital bone are quite unlike anything usually found in the infant skull at this age. No analogous condition is to be found in the higher apes. A fairly well-marked vermian fossa is found

in the lemur and the marmoset, but in the macacus monkey and cercopithecus the vermian fossa is absent.

It is suggested that this may be an instance of the manifestation of a vertebra on the cephalic side of the occipital bone. Such manifestations may be found on the outer surface but I cannot find any description of an abnormality such as this. It is possible however that the high intracranial pressure due to the hydrocephalus may have been responsible for the abnormal condition. The skull is moulded by the brain, and the increase of pressure in the lateral

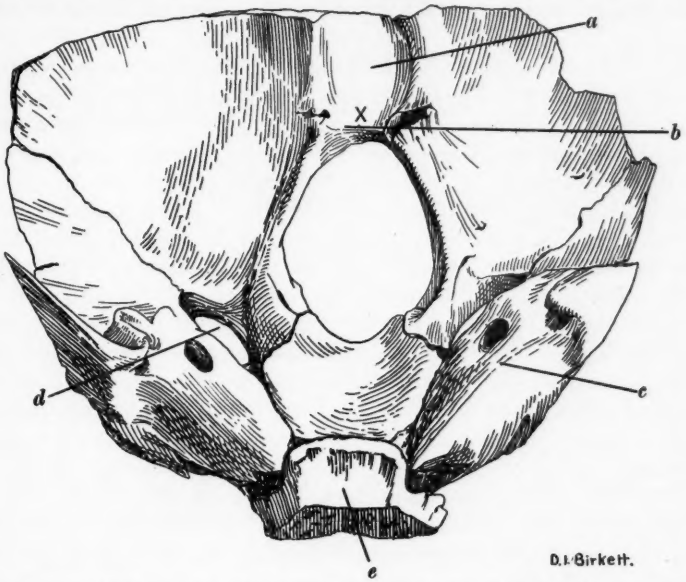


Fig. 1. Lower portion of the occipital bone and neighbouring parts of the skull viewed from above. *a*. Vermian fossa. *b*. Median interval between the two processes which mark the hinder end of the two abnormal ridges bordering the foramen magnum. *c*. Petrous bone. *d*. Jugular foramen. *e*. Body of sphenoid.

ventricles may have compressed the structures below the tentorium cerebelli and so caused the fossae in which they lie to become deeper than usual. As far as the vermian fossa is concerned, however, Davidson Black has pointed out that the vermis of the cerebellum is not normally in contact with the occipital bone in this region and has nothing to do with its formation[1].

The ridges might perhaps have been thrown into prominence by the high intracranial pressure; this seems to be the explanation of the marked projection of the semicircular canals; but this does not appear to be quite an adequate explanation for the bony formation described above, and that it may be the manifestation of a vertebra is a possible explanation.

[1] Davidson Black, "Endocranial markings of the human occipital bone." *Anatomical Record*, vol. x (1916), No. 3, p. 182.

AN EXAMPLE OF THE MUSCLE SCALENUS MINIMUS

By L. R. SHORE, M.A., M.B. (Camb.), M.R.C.P.

An example of the muscle variously known as scalenus minimus or scalenus pleuralis was found in the routine dissection of a male subject aged 60, during 1920.

The muscle arose by a fleshy belly from the transverse process of the 7th cervical vertebra on the right side, and lay deeply between the scalenus anticus in front and the scalenus medius behind. Below, it merged into a slender tendon which intervened between the subclavian artery and the inferior cord of the brachial plexus.

The tendon gained an attachment to the first rib in this position, and presented an expansion anteriorly and posteriorly which blended with the fascia of Sibson. The tendon, to some extent, intervened between the first rib and the subclavian artery, slightly raising the latter from the first rib.

The muscle was two inches in length, of which the tendon was $\frac{3}{4}$ inch.

On drawing the subclavian artery forward and the inferior cord of the brachial plexus backward, it was seen that the area on the first rib between the scalene tubercle and the insertion of the scalenus medius was definitely divided into anterior and posterior compartments. The anterior compartment corresponded to the subclavian artery, and the posterior to the inferior cord of the brachial plexus. The areas on the rib in contact with the artery and the nerve trunk were very evident owing to the presence of the scalenus minimus muscle. No abnormality in the composition of the brachial plexus was noted.

The figure illustrating the abnormal muscle was copied from a sketch made at the time.

Sebileau (1) was the first to recognise the primary significance of the muscle as a suspensor of the pleural sac.

I have many times looked for the scalenus minimus muscle, but am unable to record another in over a hundred subjects: in this instance the muscle was present on the right side only.

I have observed that it is very commonly possible to demonstrate a band of thick fascia lying in a position corresponding exactly to that of the muscle described. Sebileau and Le Double (2) insist that this band, which may be either in a fibrous or a muscular condition, is constant and normal, and that it is always associated with the pleura but may be attached to the first rib as well. This demonstration is helpful to the student in connection with the relations of the first rib. It is to be noted that the terms "sulcus subclaviae" or "subclavian groove" are still in extensive use to denote the area between the scalene tubercle and the insertion of the scalenus medius. The fact that the

main axes of the grooves anterior and posterior of the scalene tubercle would cross at an acute angle may confuse the student. This fact does not harmonise with the other fact that the subclavian vein maintains a constant anterior relationship with the artery.

The wider use of the term "sulcus nervi brachialis" (3) in amplification of "sulcus subclaviae," would be welcome in the interests of accurate description.

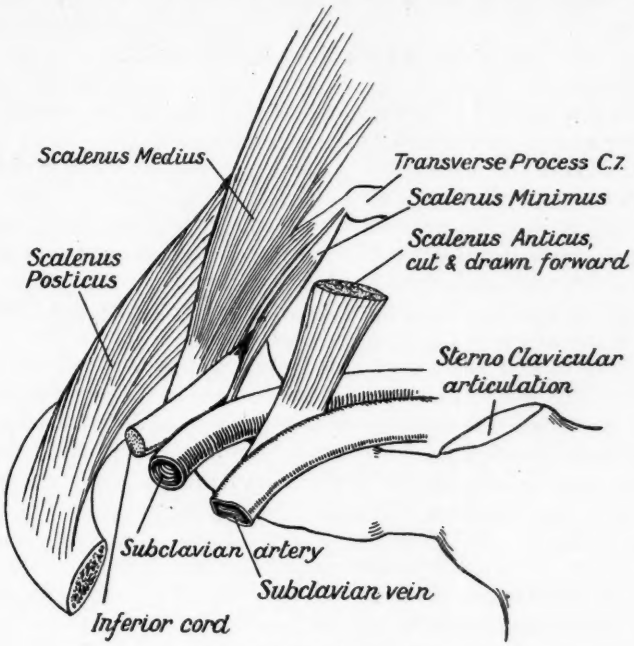


Fig. 1. Case of Scalenus minimus.

Wingate Todd (4) in "The relations of the thoracic operculum" discusses the relations of the first rib. One of his diagrams (*ibid.* p. 295, fig. 3), in which the artery was antero-superior in relation to the inferior cord of the brachial plexus, corresponds very closely to the examples here described.

Spalteholtz in the *Hand Atlas of Human Anatomy* (vol. II, 260) gives a description of the muscle, which corresponds to that described here, except for its origin from 7th cervical vertebra which is apparently unusual.

REFERENCES

(1) Le Double. *Variations du Système Musculaire de l'Homme*, I, 160.
(2) Sebileau and Le Double. *Ibid.*
(3) Wood-Jones. *Anat. Anzeiger*, XXXVI, Bd. I, 1910, 25.
4) Wingate Todd. *Journ. Anat.* vol. XLV, 294 and 295.

A CASE OF MULTIPLE ANOMALY OF THE PHALANGES OF THE HANDS IN A GIRL AGED 15

By L. R. SHORE, M.A., M.B., M.R.C.P.

This case of a bilateral deformity of the hands is recorded on account of the remarkable appearance revealed by X-ray examination.

A condition of the phalanges apparently not previously observed is here described.

The patient is a girl aged 15, a milliner's apprentice, who applied at St Bartholomew's Hospital for advice in connection with her hands, the joints of which were swollen and causing clumsiness.

The hands, except in one respect, appear quite symmetrical. There is a swelling in the region of the first interphalangeal joint in each finger. The fingers, distal to that joint, show a deviation from the straight line; in the index and middle fingers toward the ulnar side, and in the ring fingers rather toward the radial side. The little finger of the right hand deviates to the radial side, but that of the left hand is straight. The thumbs appear normal. The middle finger of the left hand is shorter than its fellow, and the shortening appears to be in its metacarpal element, judging by proximal displacement of the knuckle.

The flexion and extension movements of the fingers and thumbs are quite good. Passive movement shows that there is no undue lateral movement at the first interphalangeal joints.

Palpation does not suggest the presence of any effusion into the joint, or any thickening of periarticular tissues. The clumsiness seems to arise mainly from the "crowding" of the fingers, which is apparent even in full extension (fig. 1).

There is no history at any time of any effusion into the joints, or pain, except for chilblains. The skin is of the moist bluish character associated with deficient circulation, but chilblains apparently affected knuckles and interphalangeal joints indifferently.

The courtesy of the Secretary of the Railway Servants' Orphanage at Derby has furnished the following particulars:

> This girl was with us from September 1916 to August 1925, when she left on reaching the maximum age. The condition of her hands was noticed as peculiar when she was admitted, and on several occasions she was shown to the Doctor, but no treatment was ordered. . . . The condition of her hands made no difference to her work or her general health.

It is fortunate that the patient has been under the fairly close observation of an Orphanage since 1916, for it seems to be established that:

(1) The hands were abnormal in September 1916.

(2) At no time has any arthritis been observed.

The patient states that the fingers were straight until the 10th year, i.e. till 1920, which does not tally entirely with the observation above. Perhaps that year marks the commencement of deviation of the fingers from the straight line.

The general physical condition of the patient is good. The limbs are straight, and there are no signs of rickets or other disease. The feet are normal in appearance. The thoracic viscera are healthy.

The X-ray photograph (antero-posterior), fig. 2, reveals the following features:

(1) The epiphyses (basal) of the intermediate phalanges, as yet ununited, are flake-like and strongly concave.

(2) The base of 1st phalanx in both thumbs is concave, but no separate epiphysis is seen.

(3) The heads of the first phalanges of the fingers show some "moulding" to correspond with the concave bases of the intermediate phalanges.

(4) The intermediate phalanges are shorter than the normal in proportion to first phalanges.

(5) The middle metacarpal of the left hand is short. In this metacarpal only of the whole series, with the exception of those of the thumbs, is the epiphyseal line entirely lost.

(6) None of the joints show any evidence of arthritis.

X-ray photographs of the feet show that their skeletons are in every respect normal.

The following commentary is offered:

(1) In the absence of any past history or present evidence of arthritis, and in consideration of the symmetry, the abnormal shape of the epiphyses of the intermediate phalanges may be supposed to be a congenital abnormality.

(2) The bases of the first phalanges of the thumbs are somewhat similar. The point is of minor interest in connection with the homologies of the skeletal elements of the thumb and other digits.

The view has been put forward that the first phalanx of the thumb is equivalent of the intermediate of the fingers; the first metacarpal of the first phalanx; the basal epiphysis of the first metacarpal of the whole metacarpal of the other series.

(3) The normal intermediate phalanx has a base presenting in the middle a ridge slightly convex which runs antero-posteriorly. A stable joint is thus effected with the head of the first phalanx which has two fairly definite radial and ulnar tuberosities.

In the presence of a concavity in the lower end of the intermediate phalanx,

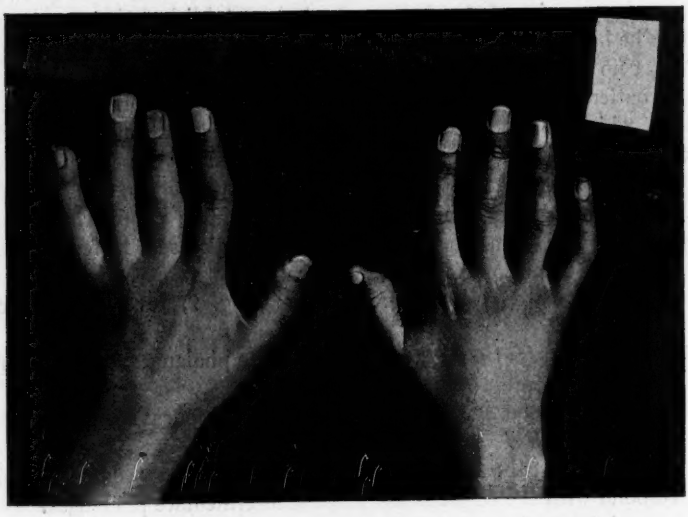


Fig. 1.

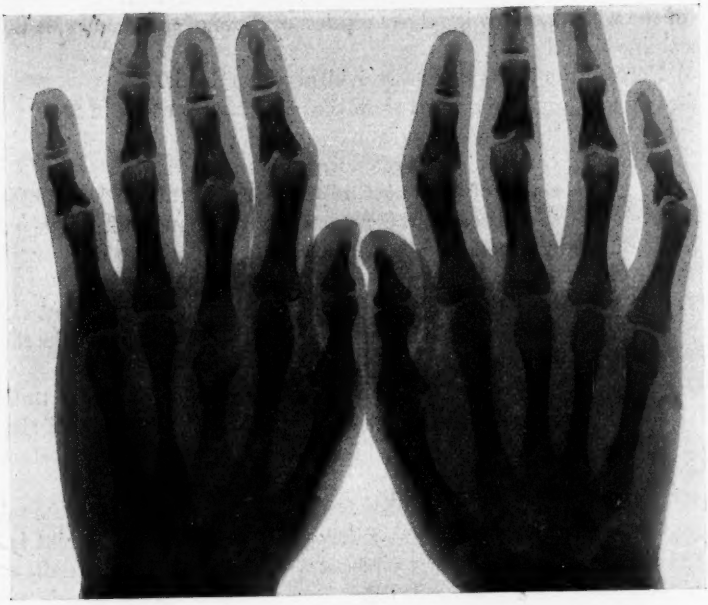


Fig. 2.

it is evident that that bone must ride on either the radial or the ulnar tuberosity for mechanical stability.

The intermediate phalanx is balanced on the ulnar tuberosity in the index and middle digits, and on the radial tuberosity in the ring and middle digits.

Fig. 3.

The exception is in the little finger of the left hand, where the phalanx is still balanced in apparently unstable equilibrium.

The deviation of the distal phalanges towards the mid-line is, no doubt, determined by the effect of the flexor tendons on the unstable balance referred

to above. The normal effect of the flexor tendons is to bring about a movement spiral rather than a true flexion.

The abnormality affords occasion for the partial dislocation seen in this case.

It may be supposed that the "moulding" of the heads of the first phalanges is a secondary effect.

(4) The proportions of the skeletal elements of these hands have been compared with a normal hand of comparable age.

The first phalanges have been selected as a basis of comparison of the lengths of the skeletal units rather than the metacarpals. These bones seem to be the most nearly normal of the series.

The nearest control available is a skiagraph of the right hand of a subject aged 14 (fig. 3). This is borrowed from the X-ray Department of St Bartholomew's Hospital, where it is retained as a normal. I wish to make all acknowledgments.

The lengths in mm. of the skeletal elements of the hands under consideration, and of the normal, are set out in Table I.

Table I.

	Case, aged 15										Normal, aged 14				
	Left					*Right*					*Right*				
Digit	V	IV	III	II	I	I	II	III	IV	V	I	II	III	IV	V
Metacarpal	52	57	{48}	65	49	48	63	59	57	53	39	58	57	51	46
Phalanx I	37	45	47	43	28	30	43	48	46	39	28	35	39	36	28
Phalanx II	17	24	24	21	16	18	21	25	24	17	21	21	24	23	16
Phalanx III	17	19	18	18			18	–	20	19		14	15	15	14

In the accompanying graph these lengths have been plotted as percentages of the lengths of the first phalanx, in a vertical direction.

Horizontal lines have been drawn on the same scale to indicate the average value of the second and third phalanges and the metacarpals relative to the first phalanx, again in percentages. On the right of the graph the corresponding values of the normal hand are plotted, and horizontal lines to indicate averages.

Measurements of the units of six skeletons of the normal adult hand have been made and averages prepared as a check on the normal: these are plotted on the extreme right.

The values of these averages are set out in Table II.

Table II

	Case, aged 15	Normal, aged 14	Measurements on Skeleton
Metacarpal	132	153	147
Phalanx I	100	100	100
Phalanx II	50	60	60
Phalanx III	42·5	42	44

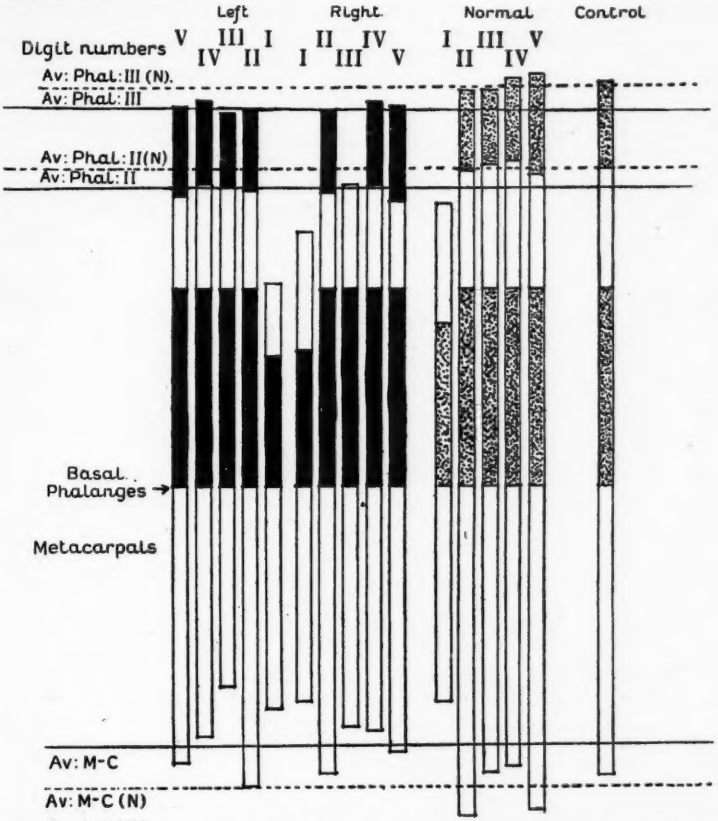
It may be presumed that the normal used here is a fair average.

In computing these averages the middle metacarpal of the left hand has been omitted.

In the graph, the values for the thumbs have been estimated as percentages of the average lengths of the first phalanges.

The following conclusions are submitted:

(1) The insignificant size of the basal epiphyses of the hands suggests a developmental error.



(2) Deformity of fingers and moulding of heads of the first phalanges are secondary.

(3) There is a relative shortening of the intermediate phalanges and of the metacarpals.

(4) In the thumbs the shortening is in the first phalanx.

(5) The remarkable symmetry, and the lack of past history or present evidence of disease, render multiple congenital abnormality the most probable interpretation of the condition.

THE MAMMALIAN OCULOMOTOR NUCLEUS

By WILFRID E. LE GROS CLARK

The literature dealing with the oculomotor nucleus of mammals has accumulated to voluminous proportions and there still remains considerable doubt regarding the localisation of function among the constituent cells of the group and even regarding the actual constitution of the nucleus itself. Of the later works dealing with these subjects, those of Brouwer (4) and Latumeten (11) give an extensive summary of the investigations of previous authors and their own conclusions remain contradictory on important questions. The former has brought in evidence culled from a detailed comparative anatomical study in order to throw light on debated points and, except for the description of the IIIrd nerve nucleus in a few animals by Bach (1), Tsuchida (15), Bernheimer (2), Panegrossi (13) and others, this method represents a new line of investigation in connection with this particular subject.

The present communication is an extension of Brouwer's observations, and was initiated as a result of a study of the oculomotor nucleus in certain lower primates and menotyphlous insectivores.

Before giving a systematic account of the nucleus in the various mammals which have been studied, it will be convenient here to indicate precisely what is meant by the oculomotor nucleus. The main portion of the nucleus is formed by two columns of large multipolar cells which lie one on either side of the median plane in the floor of the aqueductus Sylvii, extending from the posterior extremity of the IIIrd ventricle in front approximately to the level of the posterior margin of the anterior corpus quadrigeminum. These lateral nuclei (or main nuclei) have been regarded by most authorities as divisible into dorsal and ventral groups both in man and in many lower vertebrates. Posteriorly, the lateral nuclei become continuous with the trochlear nuclei, and the precise limiting boundary between the nuclei of the IIIrd and IVth nerves is not always easy to determine.

Tsuchida and Obersteiner (12) maintain that, in man, there is usually quite a definite interval, extending over two or three sections, in which there are fewer ganglion cells or even none at all. Bernheimer draws attention to the fact that between the distal extremities of the lateral nuclei of the IIIrd nerve many commissural fibres pass which disappear entirely at the proximal end of the trochlear nucleus. Biervliet (3), working on the rabbit, found no sharp division between the two nuclei. In some sections he found the cells of origin of the IVth nerve intermingling freely with those of the IIIrd nerve. He points out that a method of recognising the commencement of the trochlear nucleus when following the serial sections of this region caudally is to note

the situation of "la masse grise dans une dépression nettement accentuée du faisceau longitudinal postèrior," a depression which, he further remarks, is absent throughout the length of the oculomotor nucleus. Kolliker(10) states that the cells of the distal end of the IIIrd nerve nucleus are somewhat smaller than those of the trochlear nucleus. In my own series, I found a definite and distinct interval between the two nuclei in *Erinaceus*, and, in one of my specimens of *Tupaia* (No. 2), the cells of the trochlear nucleus have for some reason or other taken up the stain in a different manner to those of the oculomotor nucleus. In the latter instance, there is, as in the rabbit, an intermingling of the cells of each nucleus in some of the same sections. These cases in which the distinction between the two nuclei is quite obvious enable the following points to be given by which they may generally be distinguished from one another. The cells of the trochlear nucleus, relatively to those of the oculomotor nucleus, are rather more tightly packed together and form a more circumscribed, almost circular group as seen in cross-section. The lateral groups are situated further apart, lodged in a neatly defined pocket in the dorsal aspect of the posterior longitudinal bundle, and separated by a wide median raphe containing many small raphe cells,which pushes its way up towards the aqueductus Sylvii like a wedge where the oculomotor nucleus and the trochlear nucleus meet. The small raphe cells accumulate in the floor of the aqueductus Sylvii in the neighbourhood of the trochlear nucleus to form a promiment nucleus dorsalis raphae.

The lateral nuclei of the IIIrd nerve are separated as a rule by a median raphe which varies in width in different parts of the nucleus and also in different species of animals. Generally speaking, it is somewhat wider dorsally than ventrally. In the median raphe there may or may not be found large multipolar cells similar to those which constitute the lateral nuclei. The number and extent of these centrally placed large cells not only differ in different animals, but also show considerable individual variation in a single species. They may be strewn across the mid-line within no well-defined limits or they may be collected together and separated by fibre tracts from the lateral nuclei to form what appears to be a distinct and separate bunch of cells, the so-called "central nucleus of Perlia." This nucleus is present in 80 per cent. of human brains (Tsuchida), and although its presence in other mammals is generally denied (Brouwer, Bach, Tsuchida), an appearance closely resembling it may be found in some, e.g. the cat (Latumeten). There can be little doubt that the central nucleus of Perlia is derived from the large cells which are found scattered diffusely over the mid-line in many mammals, but it is best to preserve this name for a cell group definitely segregated from the lateral nuclei as the description was originally applied by Perlia(14) himself.

Placed in or close up against the mid-line in relation to the anterior extremity of the dorso-medial aspect of the lateral nuclei and extending cranially in front of the latter, is usually found a group of small cells which have been divided into the anteromedian nucleus and the nucleus of Edinger-Westphal.

Brouwer's contention that these two groups merge indefinitely into each other and that they contain identical cellular elements, and that there is thus no justification for their separation, is supported by my own investigations, and it will be convenient to refer to the whole group as the Edinger-Westphal nucleus. Brouwer gives the following criteria for the identification of this group—"dass die Zellen kleiner und weniger intensiv als die anderen gefärbt sind und dass sie dichter beim Aqueductus Sylvii liegen." These are presumably in addition to the relative position in which these cells are characteristically found. Tsuchida has further noted that the cells are poorly provided with cell processes and that their nuclei are relatively large. This author shows that in man the cells of this group vary in size in different parts of the nucleus, being largest anteriorly where they reach diameters of 17μ by 30μ as compared with the large cells of the lateral nuclei, 35μ by 40μ. As will be seen later, the size of the cells of the Edinger-Westphal nucleus, relatively to those of the lateral nuclei, also varies considerably in different animals. It should be stated that many authors believe that the Edinger-Westphal group is not a constituent part of the oculomotor nucleus proper. It is included in the description of the nucleus in this paper for reasons which will become apparent.

Tsuchida has described a group of cells situated in the dorsal part of the raphe between the posterior extremities of the lateral nuclei which he has called the "caudal central nucleus," consisting of cells which are smaller than those of the lateral nuclei. This group occupies a position which bears the same relation to the lateral nuclei posteriorly as does the Edinger-Westphal nucleus anteriorly. Little attention seems to have been paid to this group by other authors, though, as will be seen, it appears to have some phylogenetic importance.

The nucleus of Darkschewitz has not been included in the descriptions given here. It is a nucleus the limits of which are extremely difficult to define anatomically, and the evidence in support of the theory that it represents a part of the oculomotor nucleus is so slender as to be practically negligible, at least for the present.

The oculomotor nuclei of the following animals have been studied: (1) *Erinaceus*; (2) *Macroscelides*; (3) *Tupaia minor*; (4) *Galeopithecus*; (5) *Sciurus*; (6) *Ovis*; (7) *Lemur varius*; (8) *Nycticebus tardigradus*; (9) *Galago crassicaudatus*; (10) *Tarsius spectrum*; (11) *Hapale Jacchus*; (12) *Macacus* (? sp.).

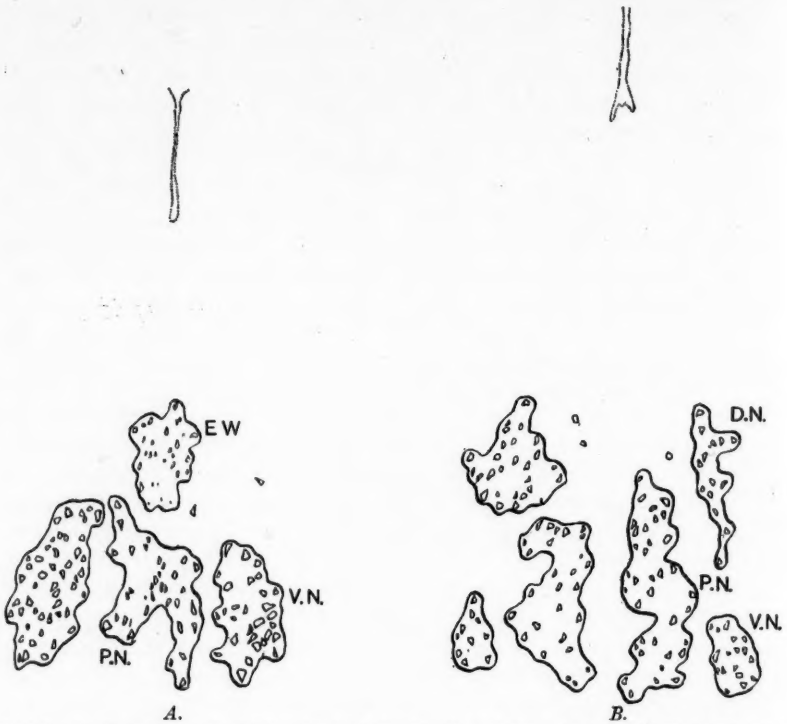
The nucleus in each has been studied by means of serial transverse sections through the mid-brain. They have been stained with toluidine blue with the exception of *Nycticebus* which was stained with paracarmine. For the loan of the sections of the brain of *Hapale* and *Tarsius* I am indebted to Dr Woollard of University College. The sections of *Nycticebus* were prepared by the late Professor Hunter for his paper dealing with the oculomotor nucleus of this animal.

Erinaceus. The oculomotor nucleus of this animal is very simple. The lateral nuclei are formed of two groups of large ganglion cells closely bunched together, lying one on either side of the median plane and separated throughout the length of the nucleus by a marked interval which is somewhat larger distally. The ventral parts of the lateral nuclei approach one another more closely than the dorsal. Distally the ventral part of the nucleus tends to broaden out a little, some of the cells straggling out along the track of the issuing fibres of the IIIrd nerve, constituting the "buchtzellen" of Bach. There is a distinct interval between the oculomotor nucleus and the trochlear nucleus, so that the boundary between the two can be readily distinguished. I have been unable to detect any definite Edinger-Westphal nucleus. Small and ill-stained cells can be seen in the median raphe, typical raphe cells, but they nowhere become differentiated or aggregated to form a recognisable nucleus. I have confirmed the absence of this nucleus by an examination of a series of transverse sections of a second brain of *Erinaceus.*

Macroscelides. The oculomotor nucleus of this insectivore is very similar to that of *Erinaceus*, the only difference being that there is a distinct Edinger-Westphal nucleus which shows the same features as that in *Tupaia.*

Tupaia minor. In comparison with the oculomotor nucleus of the two preceding species, that of *Tupaia* is clearly more elaborated. Here, again, I have studied serial sections of two brains, and the structure of the nucleus is identical in both. The cluster of small cells representing the Edinger-Westphal nucleus does not form a sharply defined group although it is readily recognisable. It commences anteriorly immediately proximal to the anterior extremity of the lateral nuclei where it begins to show itself as a specialised dorsal part of the small raphe cells that lie here between the posterior longitudinal bundles and extend ventrally between the red nuclei. It consists of small oval cells the long axes of which are disposed vertically, poorly staining with toluidine blue in comparison with the cells of the lateral nuclei. It extends back to about the middle of the oculomotor nucleus, fading away gradually when traced distally. The large-celled lateral nuclei are clearly and continuously subdivided on either side into three distinct groups, a dorsal, a ventral, and a paramedian group, all of which extend practically throughout the whole length of the oculomotor nucleus. As can be seen from the Text-figure (2), the ventral nucleus is broad proximally and extends further in this direction, becoming attenuated as it is traced distally, while the dorsal nucleus, on the contrary, broadens out posteriorly and extends further into the territory of the trochlear nucleus. The ventral nucleus can be traced directly (or with scarcely a perceptible interval) into the trochlear nucleus behind. The continuity of these nuclei may have some significance in connection with the localisation of function in the IIIrd nerve nucleus. The distinction between the cells of the IIIrd and IVth nuclei is easy to make, for the latter (in one of the specimens studied) are stained less sharply in a very conspicuous fashion. The dorsal and paramedian nuclei are continued for a little way

distal to the proximal extremity of the trochlear nucleus. The paramedian nuclei, as their name implies, lie close against the mid-line, generally between the ventral nuclei and the ventral half of the dorsal nuclei of either side. In some regions the paramedian nucleus itself shows a tendency to be subdivided again into smaller groups of two or three. Proximally the paramedian nuclei approach each other very closely and, indeed, in some sections they can be



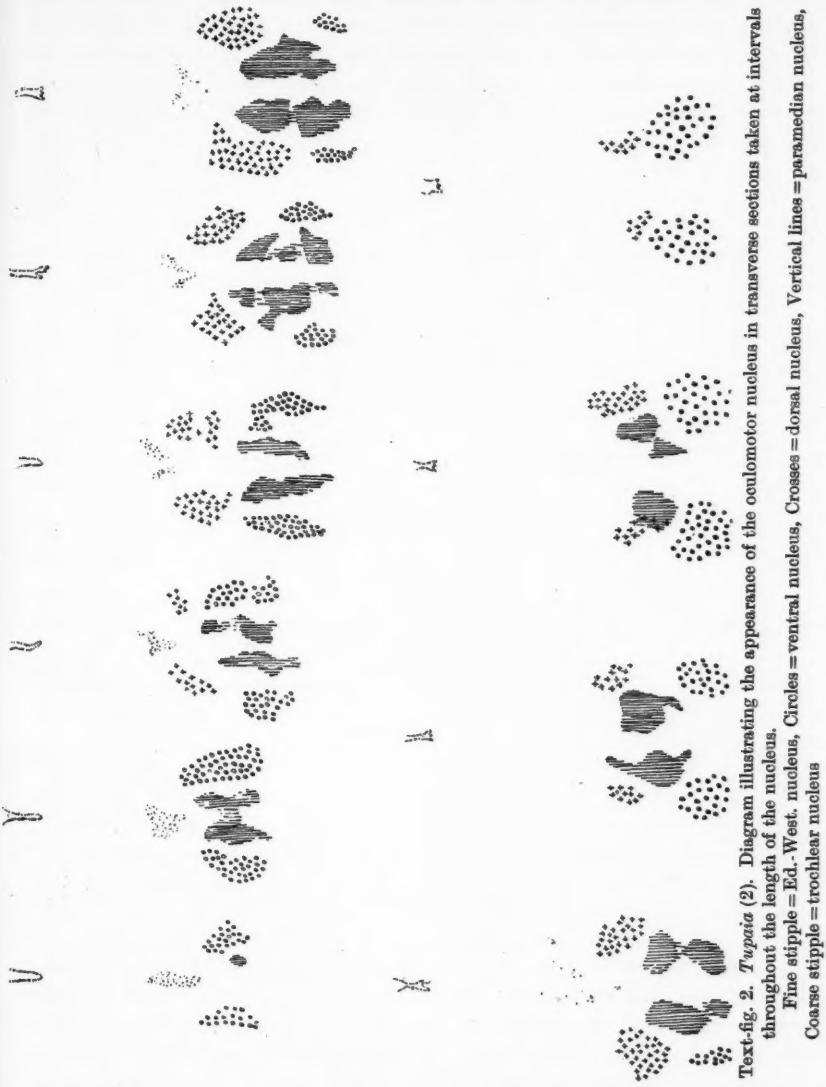
Text-fig. 1. *Tupaia* (2). *A*. Section 24–6, at the junction of the anterior and middle thirds of the nucleus. *B*. Section 28–3, at the junction of the middle and posterior thirds.

Ref. of text-figures: *D.N.* = dorsal nucleus, *V.N.* = ventral nucleus, *P.N.* = paramedian nucleus, *E.W.* = Edinger-Westphal nucleus, *C.C.N.* = caudal central nucleus.

All the text-figures represent tracings of actual sections made by means of a projectoscope.

seen to be connected by large cells which lie actually in the median plane (see Text-fig. 1 *A* and Plate I, fig. 3). Elsewhere, the nuclei are separated by a well-marked median raphe. The cells of the lateral nuclei, although segregated into the circumscribed groups just described, are on the whole spread out over a relatively broad area as viewed in cross-sections of the mid-brain. It is convenient here to draw special attention to the nucleus of this primitive animal, for although it shows a definite advance on the

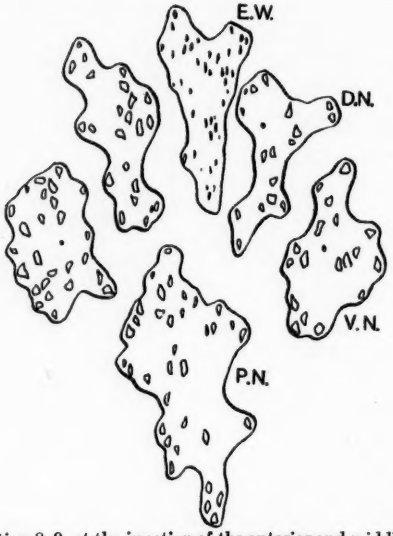
condition found in *Erinaceus* and *Macroscelides*, it is nevertheless constructed on a simple plan. The clear arrangement into three longitudinal cell groups on



Text-fig. 2. *Tupaia* (2). Diagram illustrating the appearance of the oculomotor nucleus in transverse sections taken at intervals throughout the length of the nucleus.
Fine stipple = Ed.-West. nucleus, Circles = ventral nucleus, Crosses = dorsal nucleus, Vertical lines = paramedian nucleus, Coarse stipple = trochlear nucleus

either side of the mid-line can be detected in the oculomotor nuclei of other mammals, although this arrangement becomes progressively obscured *pari passu* with the increasing elaboration of the nucleus.

Galeopithecus. The Edinger-Westphal nucleus is composed of extremely small cells which are collected to form a definite bunch in front of the lateral nuclei, here forming the anteromedian element of some authors. Traced posteriorly, the group is found to become more diffuse where it lies in relation with the lateral nuclei, so that it is difficult in this region to differentiate it from the median raphe in which it lies. At the caudal extremity of the oculomotor nucleus, small cells of a similar type appear in some numbers



Text-fig. 3. *Sciurus.* Section 8–9, at the junction of the anterior and middle thirds of the nucleus.

and form an ill-defined group which suggests a caudal central nucleus. The lateral nuclei are incompletely divided into dorsal, ventral, and paramedian groups, the latter consisting of a collection of cells somewhat detached from the main mass and lying near the mid-line. No large cells are to be found anywhere in the median plane, the median raphe being everywhere well marked.

Sciurus. The Edinger-Westphal nucleus consists of small cells which, in their structure, are very slightly differentiated from the small median raphe

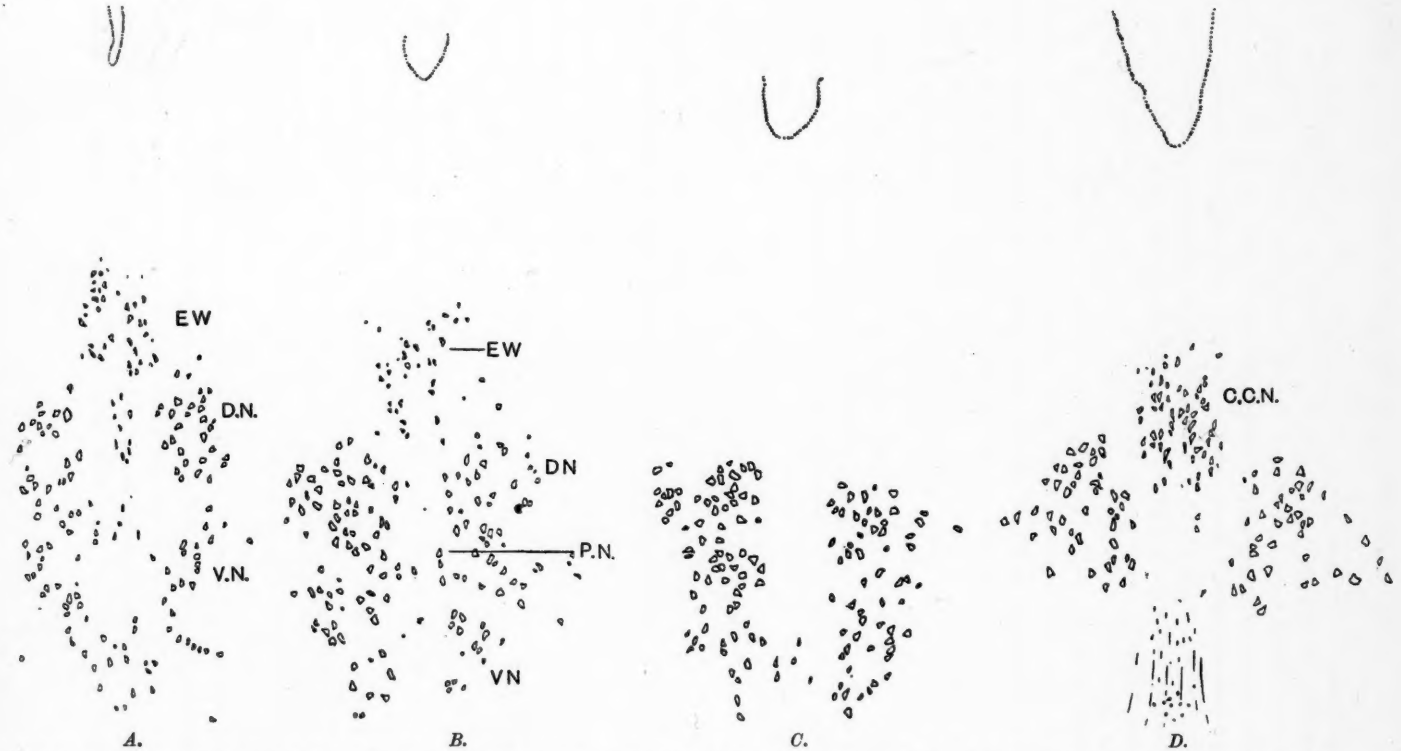
cells with which they become continuous anteriorly. The cells are situated in the median plane though tending at places to become clumped together on either side of the mid-line. Traced distally, the group is found to become apparently continuous with the nucleus dorsalis raphae which lies in association with the trochlear nucleus. Except for this latter disposition, the nucleus closely resembles that of *Tupaia*. The lateral nuclei, as in *Tupaia*, can be divided into dorsal, ventral, and paramedian groups, but the relative positions which they occupy are a little different. The paramedian nuclei are placed more ventrally relative to the dorsal and ventral nuclei. Posteriorly, however, where the ventro-laterally situated red nucleus fades away in the sections, the ventral nucleus shifts ventrally to occupy the relative position which it holds throughout in *Tupaia*. Proximally (again as in *Tupaia*) the paramedian nuclei meet and fuse in the mid-line to form a centrally disposed mass of cells on the ventral aspect of the main nuclei. Distally, the paramedian nuclei become rather bulky and are separated by a clear raphe. There is no clear distinction between the IIIrd and IVth nuclei.

Ovis. I find the nucleus of this animal to correspond to the description given by Tsuchida except that I cannot detect a distinct caudal central nucleus. The Edinger-Westphal group is little differentiated and centrally placed large cells are very few.

Tarsius. The oculomotor nucleus of this primate has already been studied by the late Professor Hunter (9). In his paper, Hunter states "The large cells form two prominent groups on each side of the median plane. Lying between these main groups are many large cells situated ventrally, which are scattered over an area including the median plane. These cells form the central nucleus of Perlia."

In my study of this nucleus, I have found some difficulty in interpreting the arrangement of subdivisions in accordance with the general plan shown in *Tupaia*, for the whole nucleus has the appearance of being compressed laterally and the cells more tightly packed together than is the case in the nucleus of the tree-shrew.

The Edinger-Westphal nucleus is conspicuously developed, in marked contrast to this nucleus in the animals already described. It commences well in advance of the anterior extremities of the lateral nuclei, and extends backwards almost as far as the posterior quarter of the whole nucleus. Throughout the greater part of its extent, it forms a group which is narrow from side to side and prolonged ventrally to separate the dorsal parts of the lateral nuclei. It consists of cells which are much more differentiated from the median raphe cells than is the case with *Tupaia*. They are distinctly larger relatively to the cells of the lateral nuclei, they are relatively more deeply stained, and they are more stellate or multipolar in form. In relation to the posterior quarter of the oculomotor nucleus, there appears a second group of small cells which, in its constitution and disposition is precisely similar to the Edinger-Westphal nucleus anteriorly, but separated from it by a clear interval. This again



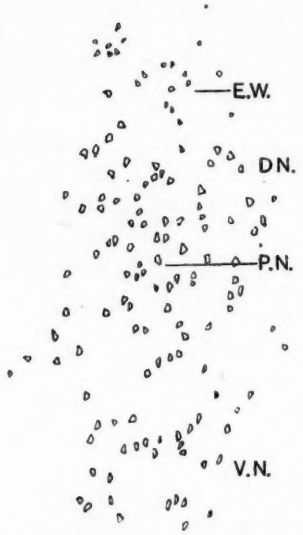
Text-fig. 4. *Tarsius*. *A*. Section 2–27, at the junction of the anterior and middle thirds of the nucleus. *B*. Section 2–55, at the junction of the middle and posterior thirds. *C*. Section 2–66, through the caudal quarter of the nucleus. *D*. Section 2–81, through the posterior extremity.

disappears when the sections are traced caudally so that there is another clear interval between it and the nucleus dorsalis raphae. This posterior small celled group is evidently the caudal central nucleus of Tsuchida, and its conspicuous development compares very remarkably with the corresponding nucleus found in *Hapale* and *Macacus*. Its close resemblance to the Edinger-Westphal nucleus (with which it is in practically continuous series except for a small interval) is to be especially noted. As regards the lateral nuclei, the division into dorsal and ventral groups can generally be recognised by an examination of the serial sections, but not in any way as clearly as in *Tupaia*. The paramedian nuclei seen so clearly in the latter are but poorly differentiated from the other cell groups of the lateral nuclei, though in some sections the cells evidently representing these nuclei are partially segregated to form a separate cell mass (see Text-fig. 4, Plate I, figs. 1 and 2). In the proximal part of their extent, the ventral portions of the lateral nuclei, as in *Tupaia* and *Sciurus*, are approximated and tend to run into each other across the mid-line. This is evidently what Hunter referred to as the central nucleus of Perlia. As this author remarks, however, this is feebly developed, and the scarcity of large cells in the median plane is very striking in *Tarsius*. It is probably to be explained by reference to the cumbersome size of the eyes of this animal, as will be seen later.

Lemur varius. The Edinger-Westphal nucleus is in no way so conspicuous as in *Tarsius*, consisting of small cells, fusiform rather than stellate in shape, and forming a diffuse group. The large-celled element consists of two lateral nuclei in which a tendency to grouping as in *Tupaia* is evident, but not clearly demonstrable in all parts of the nucleus. The lateral nuclei are separated by a median raphe in which a few large cells, ventrally placed, may be found in the proximal region. The development of this median group is strikingly poor, however, compared with the condition found, say, in the cat (Bach). At the posterior extremity of the oculomotor nucleus, in the dorsal region of the median raphe, clumps of small cells appear which resemble those of the Edinger-Westphal nucleus and which evidently represent a rudimentary caudal central nucleus.

Galago. In general appearance on cross-section, the oculomotor nucleus of *Galago* bears a close resemblance to that of *Tarsius*, but there are important distinctions. The Edinger-Westphal nucleus is small and inconspicuous, consisting of small stellate cells scattered about the mid-line in the usual situation. The cell group is so diffuse that it is difficult to say precisely where it ends when traced antero-posteriorly, but it appears to extend to about the middle of the nucleus. The lateral nuclei are elongated dorso-ventrally in the anterior two-thirds of their extent, and are here partially divisible into dorsal and ventral groups. Distally, in the posterior third, a median group of large ganglion cells appears, in some sections partially separated from the lateral nuclei between which it lies, but in most places merging into the latter on either side (see Text-fig. 6). The significance of this median group is not quite

apparent. It occupies much the same position as the caudal central nucleus in other mammals, but its constituent cells are of the large ganglionic type, and bears no resemblance to the Edinger-Westphal nucleus which is found in this animal. Moreover, the cells occupy the greater part of the median raphe in this region and are not confined to the dorso-medial aspect of the oculomotor nucleus like the typical caudal central nucleus. The supposition is either that the caudal central nucleus is not present in *Galago*, but is replaced by large cells derived from the lateral nuclei, or that the caudal central



Text-fig. 5. *Nycticebus*. Section 72–3, at the junction of the anterior and middle thirds.

Text-fig. 6. *Galago*. Section 3–3, through the caudal third of the nucleus.

nucleus in this animal is of a type very different from that found in the other mammals here studied. The former seems more probably the correct interpretation. At its posterior extremity, this median nucleus becomes surmounted by a group of small cells which, traced backwards, form a group passing dorsally to become continuous with the nucleus dorsalis raphae in the floor of the aqueductus Sylvii immediately dorsal to the trochlear nucleus.

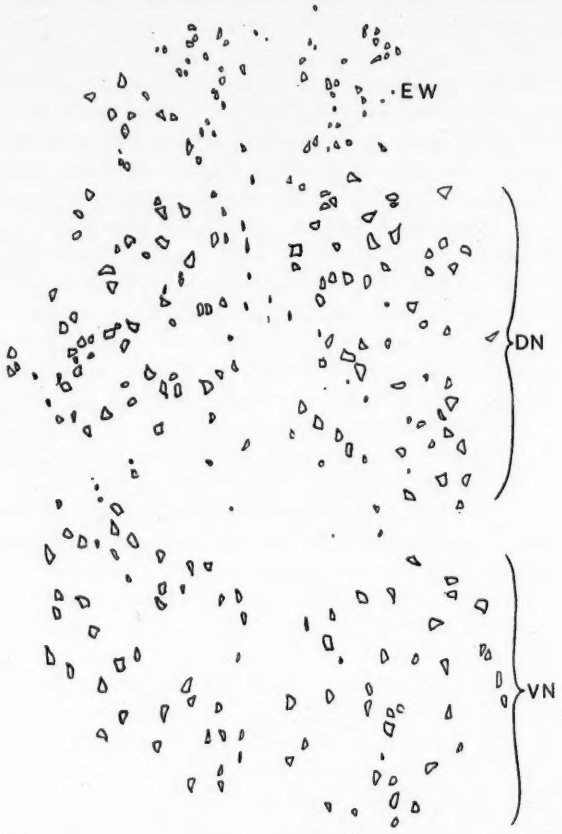
Nycticebus. For the study of the oculomotor nucleus of this animal, I have had the opportunity of examining the series of sections (stained with

paracarmine) used by Hunter for his paper. Paracarmine does not give such good facilities for an examination of the grouping of the cells as does toluidine blue, but nevertheless the details of the nucleus can readily be made out by a close study.

The Edinger-Westphal nucleus, consisting of small stellate cells which are scattered somewhat diffusely, is limited to the anterior third of the length of the oculomotor nucleus. It lies about the median plane, but shows a tendency to form lateral bunches close to the mid-line on either side. The large-celled element forms a compact mass of cells compressed laterally at the proximal end, so that in this region it is difficult to recognise any regular grouping. Traced distally, the nucleus splays out somewhat. The striking feature of this nucleus is the development of an extensive median group of large cells which intervenes between the dorsal parts of the lateral nuclei and which stretches practically from the anterior end of the oculomotor nucleus backwards as far as the posterior extremity. It may, indeed, be said that the median raphe in the region of the oculomotor nucleus is practically absent altogether (see Text-fig. 5). The central group is not marked off to form what might be called a separate nucleus but forms a link by which the lateral nuclei merge into each other across the mid-line. This astonishing development of a median nuclear group has already been remarked by Hunter (*op. cit.*). The lateral nuclei are divided into a dorsal and ventral column, but the distinction between the two is not clear in every section.

Hapale (see Plate I, figs. 4, 5 and 6). The oculomotor nucleus of this animal has been described in some detail by Bach and, more recently, by Brouwer. In its elaboration, this nucleus shows a marked advance on the condition found in those animals already described. The large cells are more widely scattered so that, in cross-section, the whole nucleus occupies a relatively larger area. The Edinger-Westphal nucleus commences slightly in advance of the lateral nuclei and consists of two groups which for the most part lie well to either side of the mid-line (though there is a tendency to fusion in the mid-line anteriorly), and which extend back to about the middle of the oculomotor nucleus. This small cell nucleus fades away very gradually, however, so that it is impossible to define its extent with any precision. It consists of cells which, compared with those of the nuclei previously described, are remarkably differentiated. Their size is only slightly smaller relatively to the cells of the lateral nuclei, they are stellate in shape and stain well. At the distal extremity of the oculomotor nucleus, in the region where this adjoins the trochlear nucleus, this small cell group reappears, precisely as has been detailed in the case of *Tarsius*. It forms here a single well circumscribed group dorso-medial to the lateral nuclei and clearly separated from the latter. Bach shows this group in his figure of Weigert preparations of the IIIrd nerve nucleus. This author, however, appears to regard the constituent cells as similar to the large ganglion cells of the lateral nuclei. This, however, is not the case, for although the difference between the cells of the lateral

nuclei and those of the Edinger-Westphal nucleus is not nearly so marked as in most other mammals, the distinction is evident enough on an examination of toluidine blue preparations. This group is clearly the caudal central nucleus described by Tsuchida. The lateral nuclei, as stated above, are somewhat diffuse. Although the division into groups is not clearly marked in every individual section, a study of the serial sections in continuity shows a dorsal



Text-fig. 7. *Macacus*. *A*. Section 6–3, at the anterior extremity of the nucleus.

and ventral group as well as an irregular collection of cells which lie medially close to the mid-line. The latter, which evidently corresponds to the paramedian nucleus so clearly defined in *Tupaia*, is better developed in the posterior part of the nucleus, forming here bunches of cells which lie close up against and in the median plane. The lateral nuclei, therefore, appear more widely separated from each other proximally than distally, and in the dorsal

part of the distal third of the nucleus, as Brouwer has pointed out, there is no clear demarcation between the right and left nuclei for they are here connected by large cells which are scattered in the median raphe. There is no central nucleus comparable to that which has been described by Perlia in the oculomotor nucleus of man.

Macacus. The oculomotor nucleus of this monkey presents a still further stage of elaboration. The Edinger-Westphal nucleus is similar to that of the marmoset, consisting of two laterally disposed groups and extending over the anterior half of the whole length of the IIIrd nerve nucleus. Here again, however, it fades away very gradually, so that its limits cannot be laid down with precision. Of the lateral nuclei, a division into dorsal and ventral groups can be recognised anteriorly, but in the greater part of the length of the

Text-fig. 7. *Macacus. B.* Section 16–6, near the posterior extremity.

nucleus such a division cannot be detected. Proximally, the lateral nuclei consist of two circumscribed columns of cells elongated dorso-ventrally and separated by a very narrow median raphe. In the latter, odd cells of the large ganglionic type may be found scattered very sparsely, more especially in the ventral part of the raphe. These may serve in certain sections to link up partially the lateral nuclei of the two sides but they by no means obliterate the raphe which separates the lateral nuclei, and they do not form a definite cell group. Distally the lateral nuclei become more irregular in shape, many cells being squeezed out between the fasciculi of the posterior longitudinal bundle along the track of the issuing fibres of the IIIrd nerve. Here the median raphe becomes somewhat broader. In the region of the distal third of the nucleus, a group of small cells appears dorso-medially to the lateral

nuclei, which, if traced backwards, comes to lie immediately ventral to the nucleus dorsalis raphae. In sections stained with toluidine blue, it can be seen that this nucleus is quite distinct from the lateral nuclei; it consists of cells which are smaller and of a different type to those of the lateral nuclei, but larger than those which form the nucleus dorsalis raphae. The cell group resembles in its position and constituent cells the Edinger-Westphal nucleus except that the cells tend to be slightly larger. This is the caudal central nucleus, and clearly corresponds to the similar nucleus already described in *Tarsius* and *Hapale.*

DISCUSSION

The details obtained from a study of the oculomotor nuclei of the foregoing animals may best be discussed by reference to the individual component parts of the cell group.

The Lateral Nuclei. These groups exhibit no marked variation in regard to the type of the component nerve cells. In *Erinaceus* and *Macroscelides*, each lateral nucleus forms a simple circumscribed column of large cells stretching antero-posteriorly on one side of the median raphe, and separated posteriorly by a definite interval from the trochlear nucleus. In all other mammals studied the group is more elaborated, and, in most cases, it can be more or less definitely subdivided into a dorsal nucleus and a ventral nucleus. Such a subdivision is most distinctly evident in the simply constructed oculomotor nucleus of *Tupaia.* This fundamental division into dorsal and ventral nuclear groups accords with the description of the lateral nuclei previously given by Perlia (*Homo*), Tsuchida (*Homo*, *Macacus*), Latumeten (cat), and others, though some authors such as Edinger and Kolliker regard the lateral nucleus of man as forming a single anatomical unit. Tsuchida, however, on page 2 of his monograph, gives several reasons which indicate that such a primary division is really valid, these reasons being based on morphological and embryological data.

In the case of *Homo* and *Macacus*, Tsuchida describes the dorsal nucleus as commencing anteriorly caudal to the proximal extremity of the ventral nucleus, and terminating posteriorly by merging with the ventral nucleus. From this description it appears that the dorsal nucleus is somewhat shorter than the ventral, and that it is the ventral which becomes more or less directly continuous with the trochlear nucleus. In the case of *Tupaia*, in which the separation of the oculomotor nucleus into secondary groups is so manifest, this relative disposition of the dorsal and ventral nuclei is very evident, except that here the two nuclei do not fuse caudally; the dorsal nucleus remains independent of the ventral and fades away as the serial sections are traced backwards, while the ventral nucleus runs directly into the trochlear nucleus.

In the descriptive part of this paper there has been described in the lateral group of the oculomotor nucleus of several mammals a paramedian nucleus,

likewise composed of large multipolar cells. This lies up against the median raphe, tending in some regions to merge with that of the opposite side across the mid-line. This nucleus, again, is strikingly evident in *Tupaia*. There can be little doubt that the centrally situated large cells found in the median raphe in many mammals, including even the central nucleus of Perlia in man, are derived from this portion of the oculomotor nucleus. That this paramedian nucleus is not easily recognisable as a separate group in some mammals possessing a well-developed oculomotor nucleus, would appear to be due to extraneous factors (in part at least) which tend to distort and obscure the primary simple arrangement. The evidence of comparative morphology adduced here seems to point to the fact that a single, homogeneous lateral large-cell group of the oculomotor nucleus (as represented in *Erinaceus*) becomes separated into three subsidiary columns, dorsal, ventral, and paramedian; then, with the progressive elaboration and increasing complexity of the oculomotor nucleus, associated possibly with such factors as the crowding together of the cells by surrounding structures (e.g. the posterior longitudinal bundle), these constituent parts become more and more difficult of recognition as anatomical subdivisions capable of ready identification.

The width of the median raphe separating the oculomotor nuclei on either side varies somewhat in different animals. Generally speaking, the nuclei are separated by a wider interval in cases in which they are simply constituted, in those mammals, for example, whose eyes are disposed laterally and are not capable of complicated conjugate movements. There is, however, no strict correspondence between the approximation of the lateral nuclei and the degree of ocular convergence in individual species.

The Nucleus of Convergence. Perlia described in 1889 an almond shaped, large celled median nucleus situated in the region of the proximal third of the oculomotor nucleus of the human brain. Many authors have also observed the large multipolar cells scattered diffusely over the median raphe and Brouwer has lately drawn particular attention to those which lie in the region of the posterior half of the oculomotor nucleus in some mammals, connecting up across the mid-line the two lateral nuclei. In furtherance of the conclusions of Knies, Stuelp, Majano, von Monakow and Edinger, Brouwer believes that both the central nucleus of Perlia and the scattered median large cells are related to the internal recti muscles and subserve the movement of convergence. These conclusions have been in part confirmed by the recent work of Latumeten. It should be emphasised again that the central nucleus of Perlia—in the form in which it was originally described—is probably only to be found in man (Bach, Brouwer, etc.).

My own investigations show that in some animals in which the power of ocular convergence must be very limited, e.g. *Sciurus*, *Tupaia*, there is a tendency for the paramedian groups of the lateral nuclei to meet and intermingle in the ventral part of the raphe in the anterior third of the oculomotor nucleus—in a corresponding region, in fact, to that in which the nucleus of

Perlia is found in man. In some mammals, e.g. *Hapale*, *Galago*, the dorsal region of the raphe in the caudal third of the oculomotor nucleus is occupied by abundant large ganglion cells which here link up the lateral nuclei of either side. In other animals, such as *Nycticebus*, the cat (Bach), the median large cells extend throughout the greater part of the oculomotor nucleus, so that the median raphe is practically obliterated.

Against Brouwer's contention that these median cells are essentially associated with convergence of the eyes and binocular vision, my own findings raise three arguments:

1. Median large cells are found in the oculomotor nucleus of *Tupaia* and *Sciurus*, animals whose eyes are laterally disposed and therefore associated with a minimum degree of binocular vision.

2. In *Tarsius*, centrally placed large cells are almost absent altogether.

3. The degree of development of this median group in individual species bears no relation to the degree of binocular vision of which the species appears capable.

It is necessary here to examine these arguments more closely.

1. The presence of an internal rectus (or anterior rectus) muscle in mammals generally, suggests that even animals whose eyes are disposed laterally may be able to converge to a certain extent. Brouwer, indeed, refers to Dexler's work on the horse, in which it is shown that this animal can fix an object with both eyes up to a point 1–1½ metres in front of the tip of the nose, but he further quotes and agrees with Ablaire that this phenomenon cannot properly be called convergence, but should be rather termed "Divergenzverminderung." It is difficult, however, to see any essential distinction between this movement in the horse and the movement of convergence in an animal such as the cat. If the identity of these two movements be granted, there can be no reason why a representative of a convergent nucleus should not be found in mammals whose vision is of the panoramic type. And, as a matter of fact, centrally placed large cells have been found, as shown above, in *Tupaia* and *Sciurus*. This argument, therefore, does not necessarily indicate that large cells found in the median raphe are not associated with convergence, but it opposes the contention that they are essentially and solely associated with a conspicuous development of binocular vision.

2. The practical absence of median large cells in *Tarsius* might reasonably be ascribed to the fact that with such large eyes this animal cannot indulge in free ocular movements. Woollard (16) has shown that the ocular muscles are small and are attached relatively far back on the sclera, and further that anatomical indications of a compensatory freedom of movement of the head are evident in the region of the occipito-vertebral articulation. But this author has also described a specialised spot in the retina of *Tarsius* which he terms a "primordium maculae," and which clearly implies the faculty of fixation of an object with accompanying ocular convergence. My own observations (5) on the living tarsier are consistent with these anatomical data.

While, therefore, the general lack of complexity, which is at first sight not a little puzzling in the oculomotor nucleus of *Tarsius*, may be explained by reference to the lack of free ocular movement dependent on the large size of the animal's eyes, the almost complete absence of centrally placed large cells is not compatible with Brouwer's hypothesis.

3. The validity of this argument is apparent from the descriptions of the nuclei of individual animals which have already been given. Of all the species examined, large raphe cells are most extensively developed in *Nycticebus*, so that in this animal, in practically the whole extent of the nucleus, there is no sharp division between the right and left lateral nuclei. Judging from Bach's description and figures (and Brouwer confirms them), the oculomotor nucleus of the cat agrees in this respect very closely with that of *Nycticebus*. It is clear that binocular vision and movements of convergence are not to be found the most highly developed in these two mammals. Again, there is no reason to suppose that *Lemur* is inferior to the cat in respect of these ocular functions, and yet in the former the median element of large cells is poorly developed. As a further example, we may point out that the median cells are more numerous in the marmoset than in *Macacus*. It is relevant here, also, to draw attention to the great individual variability shown by this median group in any one species, and man himself is not immune from such individual fluctuations. Tsuchida studied the oculomotor nucleus in over 30 human brains, and found a true nucleus of Perlia absent in 20 per cent. He also found considerable differences in the development of scattered median large cells in the oculomotor nuclei of eight Macaque monkeys.

These data, showing the lack of any direct relationship between the extent of this median group and the degree of binocular vision of which the individual animal is capable, afford presumptive evidence that there is no justification for applying to it the unqualified term of the "nucleus of convergence."

It is true that, generally speaking, large cells are found in the median raphe more especially in the case of animals capable of binocular vision, and that they are usually absent or very sparse in those whose eyes are disposed laterally. In the former, however, the oculomotor nuclei are almost without exception greatly elaborated, in association with the more precise and complicated conjugate movements of the eyes which are necessarily associated with binocular vision and the fixation of objects on corresponding points of the retina. With the growing complexity and the increase in the number of large cells which are thus to be expected in the oculomotor nucleus under these conditions, it is evident that these must find room to accommodate themselves. The nucleus is limited above by the cerebral aqueduct and hedged in laterally and ventrally by the fasciculi of the posterior longitudinal bundle. The nucleus can therefore only expand in the region of the median raphe, and the cells which will be displaced to this position will, for obvious topographical reasons, be those which lie on the medial aspect of the lateral nuclei and which thus form part or whole of the paramedian groups. If these medial cells are

associated mainly with the fibres of the IIIrd nerve which pass to the medial rectus muscle (and there is experimental and clinical evidence which indicates this to be the case), then the large cells found in the median raphe of certain mammals will necessarily have the same function. It is clear, however, that the cells attain a median position not in virtue of their association with the movement of ocular convergence, but merely as an incidental result of the general elaboration of the oculomotor nucleus which is inevitably associated with the swinging forward of the eyes from a lateral to a frontal position in the head.

The Edinger-Westphal Nucleus. The descriptive part of this paper will have shown that the surest criterion of this nucleus refers to its characteristic position and the size of its cells relative to those of the lateral nuclei. The type of the individual cells varies considerably in different species, and this fact serves to explain why so many contradictory statements have been made regarding the presence of this small celled element in mammals other than man. That the median small celled groups described in connection with the oculomotor nuclei of the different animals here studied are homologous with each other becomes evident when they are examined in series, and the even transition from more or less undifferentiated raphe cells to the well-defined cell group found in higher primates is apparent.

In *Erinaceus*, no definite Edinger-Westphal group can be identified. In the other non-primate mammals the nucleus is relatively ill-defined and formed of simple small fusiform cells which stain feebly. In *Nycticebus* and *Galago*, the component cells are somewhat better developed, but the group still remains relatively undifferentiated and small, and not by any means sharply circumscribed. In *Tarsius*, it becomes much more conspicuous, and not only is the group more extensive but the individual cells are larger relatively to those of the lateral nuclei, they are more stellate, and they stain more deeply. In *Hapale* and *Macacus*, the cell group is very distinct and shows a greater tendency to become separated into two groups, one on either side of the mid-line. The evidence derived from this comparative study indicates that the nucleus assumes a much greater importance in the anthropoidea and *Tarsius*, animals which surpass all others in the degree of differentiation of their visuo-receptive apparatus. This is a fact which must be taken into consideration when the question of assigning a particular function to the Edinger-Westphal nucleus is raised. Whatever the function may be, the elaboration of this nucleus *pari passu* with the general elaboration of the main oculomotor nucleus would seem to indicate that they are closely associated.

Brouwer, it should be noted, found a small celled element in all the mammals which he examined, though in members of the Pinnepedia and the Cetacea, the cells were very diffuse and formed no circumscribed group. Zweig(17) found the Edinger-Westphal nucleus best developed in man, and among the lower animals in the anthropomorpha, while in rodents it is very feebly developed. He also states that it is extremely variable. He found the

nucleus medianus anterior (which many authors regard as the cranial extension of the Edinger-Westphal nucleus) in all the mammals studied with the possible exception of *Phocaena*. On purely comparative anatomical grounds, Zweig concludes that the Edinger-Westphal nucleus represents a nucleus of accommodation and the anteromedian nucleus a centre associated with pupil reaction. Such a conclusion, however, is not altogether convincing, for the great degree of individual variation exhibited by these nuclei render it very difficult to estimate with any accuracy their relative development in different species.

The Caudal Central Nucleus. This nucleus was first described by Tsuchida. In my series, I have found such a cell group clearly apparent only in those animals in which the Edinger-Westphal nucleus is well developed, i.e. in *Tarsius* and the anthropoidea. Moreover, the constituent cells of the caudal central nucleus of the individuals of these two groups in each case closely resemble those of the Edinger-Westphal nucleus of the particular species, except that they show a tendency to be a little larger. It appears that the former cell group lies in series with the latter and this is especially obvious in the case of *Tarsius* in which the interval between the two is very slight, corresponding to a few sections only. Also, the development of the one seems to proceed *pari passu* with that of the other. These facts suggest very forcibly that both these nuclei have a similar physiological significance, whatever that may be. It must be noted, however, that the condition found in *Galago* (see above) suggests the possibility that the caudal central nucleus may in some cases be composed of elements of quite a different type, approximating to the type of which the lateral nuclei are composed.

General

A general survey of the oculomotor nuclei studied in connection with the present communication is, in a manner, somewhat disappointing. The variations from one species to another, bearing no obvious relation to functional needs, are numerous, and, taken together with the large degree of individual variation in animals of the same species as indicated by Tsuchida, this makes it very difficult to reduce them to a uniform type of a simple kind. The general elaboration of the nucleus in association with increasing complexity of ocular movements is evident enough, however, and this elaboration seems to involve both the large and the small celled elements.

The Localisation of Function in the Oculomotor Nucleus. In a purely morphological study, no definite statements can be made in connection with this problem. It is permissible, however, to review the results of experimental observations in order to see how they fit in with the facts of comparative anatomy.

The origin of the oculomotor fibres which innervate the intrinsic ocular muscles has led to a very considerable controversy. The assumption that the Edinger-Westphal nucleus is the nucleus of accommodation has been

negatived by the work of a number of investigators. A comparative anatomical argument against this theory, based on the assertion of some authors that the Edinger-Westphal nucleus is present in only a few mammals has been disposed of by Brouwer and Zweig, and except that I have been unable to find this group in *Erinaceus*, my own observations agree with these authors. The recent detailed work of Latumeten, however, seems to have proved beyond all doubt that the cells of this group give rise to no fibres which pass direct to the ciliary ganglion or the eye itself. From the data of comparative anatomy, it is not possible to infer more than that this small celled element bears a close relation to the oculomotor nucleus.

As regards the large celled element of the oculomotor nucleus, the schemes for the localisation of the ocular muscles therein drawn up by different authors are at great variance not only in regard to the positions assigned for the different muscles but also in regard to the degree of separate localisation. In connection with the latter, some investigators maintain that the physiological localisation of each extrinsic muscle supplied by the IIIrd nerve is fairly distinct in the nucleus, while others (e.g. Frank) hold that there is no real localisation and that each muscle receives fibres which are derived from all parts of the nucleus. The balance of evidence seems to be in favour of a certain degree of localisation. The lack of agreement among the various schemes, however, is at first sight somewhat discouraging to this idea. But these disharmonious results concern chiefly the question of antero-posterior localisation, and if one searches among the observations of the authors of these schemes for evidence of a localisation in a dorso-ventral direction, one finds more concurrence of opinion.

So much is this the case, indeed, that one is led to suspect that the functional elements of the oculomotor nucleus are more probably arranged dorso-ventrally than antero-posteriorly. Thus the observations of Van Biervliet (on the rabbit), Bach (on the rabbit), and Bernheimer (on the monkey), while they are not in agreement in respect of the antero-posterior arrangement of these elements, do agree in referring the origin of the fibres to the superior rectus and the inferior oblique to the dorsal part of the cell column and the inferior rectus to the ventral part. Starr's investigations likewise indicated that the sup. rectus and the inf. oblique are innervated from the dorso-lateral group of large cells and the inferior rectus from the ventro-mesial group. Kahler and Pick add further confirmation to these ideas by their description of a case of paralysis of the levator palpebrae, sup. rectus, and inf. oblique associated with a lesion involving the dorso-lateral bundle of nerve roots, and this evidence is again partially supported by Leube. These data suggest that the dorsal group of the main part of the oculomotor nucleus is associated with upward movements of the eye and the ventral group with downward movements. That the localisation is somewhat of this order is supported by the almost diagrammatic arrangement in *Tupaia*, in which the dorsal and ventral groups are so clearly defined, and the latter is found to become continuous

with the trochlear nucleus which also controls a downward movement of the eye. If this interpretation of the facts is correct, it remains to define the significance of the third fundamental element of the mammalian oculomotor nucleus, the paramedian group and its derivative, the central nucleus of Perlia. Brouwer produces clinical evidence to show that this is associated with the internal rectus muscle and further cites a number of competent authorities in support of this view—Knies, Stuelp, Majano, von Monakow, Starr, Edinger. Indeed, the total evidence in favour of this hypothesis appears to be strong. It seems reasonable to infer, then, that there may be a localisation of movement rather than individual muscles in the oculomotor nucleus, inward movement being represented in the paramedian group of cells, dorsal movement in the dorsal group, and ventral movement in the ventral group. Such an interpretation serves to harmonise the otherwise divergent results of a large number of observers, and is also compatible with the data of comparative anatomy.

SUMMARY

1. The description of the oculomotor nuclei of a number of mammals has been detailed.

2. Evidence has been brought forward to indicate the fundamental division of the large celled element into dorsal, ventral and paramedian groups.

3. Centrally placed cells derived from the paramedian group are found in association with a general elaboration of the oculomotor nucleus, and their presence is not directly associated with binocular vision and convergence.

4. The Edinger-Westphal nucleus (which, following the example of Brouwer and others, has been taken in this communication to include what has been regarded by some authors as a separate nucleus, the nucleus medianus anterior) shows considerable variability in its size and in the nature of its constituent cells. Generally speaking, however, it becomes elaborated *pari passu* with the elaboration of the main part of the oculomotor nucleus and of the visual apparatus as a whole.

5. The caudal central nucleus bears a close relation in its disposition and development to the Edinger-Westphal nucleus in different species.

6. The problem of localisation of function in the oculomotor nucleus has been briefly reviewed in the light of the morphological evidence derived from this investigation.

DESCRIPTION OF PLATES

Fig. 1. Transverse section through the oculomotor nucleus of *Tarsius* at the junction of the anterior and middle thirds.

Fig. 2. Transverse section through the oculomotor nucleus of *Tarsius* at the junction of the middle and posterior thirds.

Fig. 3. Transverse section through the anterior third of the oculomotor nucleus of *Tupaia* (1), showing the Edinger-Westphal nucleus, and the paramedian nuclei fusing in the mid-line.

Fig. 4. Transverse section through the anterior third of the oculomotor nucleus of *Hapale*, showing the Edinger-Westphal nucleus divided into two bilateral groups.

Fig. 5. Transverse section through the middle third of the oculomotor nucleus of *Hapale*. A well-developed paramedian group of large cells is seen here which has displaced the dorsal group of the lateral nucleus somewhat outwards.

Fig. 6. Transverse section through the distal third of the oculomotor nucleus of *Hapale*, showing the small celled caudal central nucleus.

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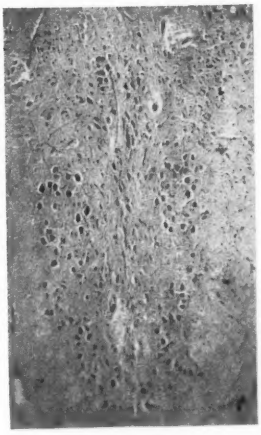

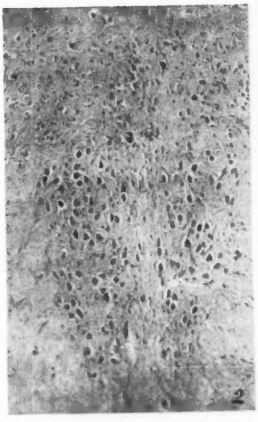

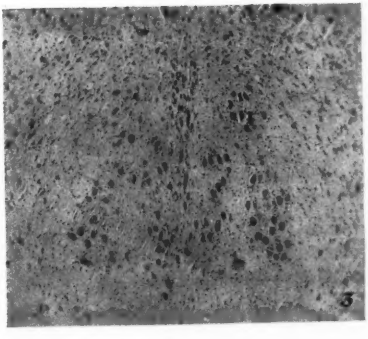

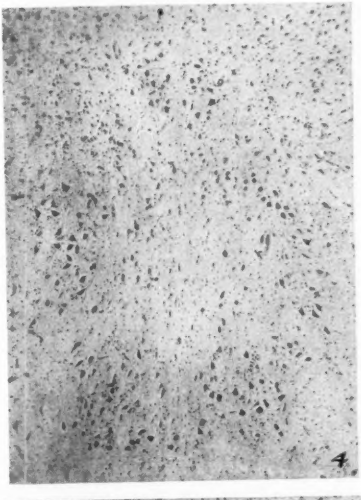

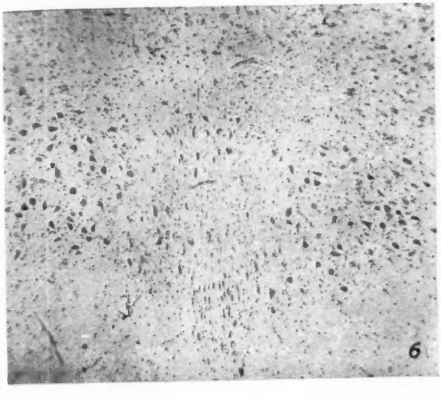

CONTRIBUTION À L'ÉTUDE DU DÉVELOPPEMENT DU CERVEAU DE L'OURS BRUN (*URSUS ARCTOS* L.)

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Ce mémoire fait suite à celui que l'un de nous a consacré avec F. Coupin à l'étude du cerveau de l'Ours nouveau-né[1], travail contenant aussi la description du cerveau de l'Ours adulte. Nos présentes recherches portent sur deux cerveaux de jeunes *Ursus arctos* L.

No. 1921—4, jeune ♂ âgé de 20 jours.

No. 1921—5[2], jeune ♀ âgée de 22 jours.

Il nous a paru indispensable de rappeler brièvement tout d'abord, d'après le mémoire cité, la description du cerveau de l'*Ursus arctos* L. à l'âge adulte et à la naissance.

I. LE CERVEAU DE L'*URSUS ARCTOS* L. ADULTE[3]

1°. *Rhinencéphale*

Le rhinencéphale de l'*Ursus arctos* L. est beaucoup plus complexe que celui des Carnassiers de moindre volume somatique.

L'angle de coudure des rhinales est très fermé et la pointe extrême de la rhinale postérieure dépasse toujours la face externe de l'hémisphère se poursuivant sur sa face inférieure, et, même, sur sa face interne.

Le tubercule olfactif est volumineux présentant à sa surface un ensemble de saillies caractéristiques.

Sur le gyrus olfactorius lateralis sont de nombreux plis orientés dans l'ensemble d'avant en arrière. Celui de ces plis qui se trouve situé immédiatement en avant de l'angle de coudure des rhinales est vraisemblablement l'incisura olfactoria persistant ici à l'âge adulte.

Le gyrus intermedius est bien distinct.

[1] R. Anthony et F. Coupin, "Le cerveau de l'Ours nouveau-né," *Album Societatis Scientiarum Svcenkianae ucraïnensium Leopoldiensis*, 1873–1923.

[2] Ces numéros sont ceux du registre d'entrée au laboratoire d'Anatomie comparée du Muséum national d'Histoire naturelle (Paris).

[3] Pour la figuration voir le mémoire précité de R. Anthony et F. Coupin. Voir aussi, pour la description du cerveau des Ursidés adultes, G. Elliot Smith, *Descriptive and illustrated Catalogue of the physiological series of comparative anatomy contained in the Museum of the Royal College of Surgeons of England*, 1902, vol. II, pp. 277–284, et les autres ouvrages cités dans le mémoire de R. Anthony et F. Coupin.

Le gyrus ambiens présente un ensemble de sillons dont deux, plus ou moins parallèles à la rhinale postérieure, paraissent être constants.

Le gyrus lunaris est bien visible et le sillon qui le limite en dehors (sulcus semiannularis) bien indiqué.

Contrairement à ce que l'on observe chez les Carnassiers de petite taille, le gyrus dentatus présente une denticulation surtout bien marquée dans sa partie inférieure et dans sa partie supérieure.

Le gyrus Andreae Retzii est très développé confluant largement en bas avec le gyrus fornicatus.

Le gyrus fasciolaris est au contraire très étroit.

Le gyrus intralimbicus est bien visible entre le gyrus dentatus et la fimbria à leur origine.

Le gyrus transversus areae piriformis est extrêmement développé[1].

On constate un début de recourbement en dedans et sur elle-même de la partie terminale du lobe piriforme. C'est une ébauche de la disposition qu'on constate, beaucoup plus accentuée, chez l'Homme et chez les Anthropoïdes, et, sur laquelle, en ce qui concerne les Primates, Mutel[2] a eu bien raison d'insister.

2°. *Néopallium*

De même que son rhinencéphale, le néopallium de l'Ours brun est remarquable par la complexité de ses plissements.

Ses grandes caractéristiques sont: 1° l'existence d'un véritable complexe sylvien répondant à l'operculisation d'une partie du territoire central; 2° l'existence d'un lobe temporal déjà constitué, en rapport avec cette operculisation; 3° l'amorce d'un lobe occipital; 4° l'accentuation de la flexion télencéphalique qui se traduit, comme nous l'avons vu, par une plus forte coudure des rhinales.

La partie du territoire central operculisée chez les Ours est comme l'on sait, la circonvolution I de Leuret toute entière, de telle sorte que le sillon d'operculisation est l'ectosylvia (Turner, Holl, Elliot Smith).

La pseudosylvia, sillon axial de la circonvolution I operculisée, et qui aborde les rhinales un peu en avant de leur point de coudure, est bien visible au fond du complexe sylvien.

La suprasylvia est le premier sillon concentrique au complexe sylvien. R. Anthony et F. Coupin ont observé sur un hémisphère droit (No. 1911—216, ♂) une interruption de la suprasylvia dans sa région antérieure.

En avant du complexe sylvien, la présylvia se continue avec l'ectosylvia.

L'orbitaire est très réduit se branchant sur la rhinale antérieure.

Le corono-latéral est généralement continu.

L'ento-latéral et le vertical sont bien marqués.

[1] R. Anthony et F. Coupin, "Le gyrus transversus areae piriformis du cerveau des Carnassiers," *Journal of Anatomy*, Jan. 1925.

[2] M. Mutel, *Études morphologiques sur le rhinencéphale de l'Homme et des Mammifères*, Nancy, 1923.

Le crucial est fortement accusé.

L'ansatus, situé en arrière du crucial, est tantôt indépendant du coronal, tantôt confluant avec lui par une de ses branches.

Le précrucial est profondément marqué, tantôt indépendant du crucial, tantôt confluant avec lui; ces deux sillons, crucial et précrucial circonscrivent à la face supérieure du néopallium une aire losangique (losange ursin) caractéristique des Fissipèdes arctoïdes et des Pinnipèdes. Il est le plus souvent coupé transversalement à partir du bord mésial de l'hémisphère par un court sillon, le bissector.

En arrière de la branche postérieure du corono-latéral, sont les sillons paracaudaux dont la présence indique le début où l'amorce d'un lobe occipital. Sur la face interne, la calcarine est très profonde. Elle se continue parfois en haut avec l'intercalaire. De même, elle se jette parfois en bas, dans le sulcus ursinus, mais, en écartant les lèvres de ce dernier, on peut toujours apercevoir un pli de passage qui marque l'indépendance des deux sillons. A l'extrémité supérieure de la calcarine se branche un petit sillon dirigé vers l'angle postéro-supérieur de l'hémisphère et qui est peut-être l'analogue de la rétro-calcarine des Primates (R. Anthony et F. Coupin). Son existence paraît être en rapport, comme celle des paracaudaux sur la face externe, avec l'ébauche constituée d'un lobe occipital.

Le sulcus ursinus qui n'est pas particulier aux Ours, comme le fait observer Elliot Smith[1], puisqu'on en retrouve l'ébauche chez d'autres Carnassiers de taille plus petite, est un court et profond sillon. Il semble quelquefois se jeter dans la calcarine, et, sa lèvre postérieure operculise quelquefois aussi l'extrémité de la rhinale postérieure.

Le collatéral (paracalcarine) croise en sautoir la marge postérieure de l'hémisphère et s'achève en bas non loin du bord libre de la lèvre postérieure du sulcus ursinus.

Le splénial, le genualis et le rostral sont bien indiqués.

En résumé, chez l'Ours brun, le rhinencéphale et le néopallium sont remarquables par la complexité de leurs plissements, celle-ci étant en rapport avec le grand volume du cerveau, en rapport lui-même avec le grand volume somatique.

Le cerveau de l'*Ursus maritimus* Desm. ne diffère que par de légers détails de celui de l'*Ursus arctos* L.

II. LE CERVEAU DE L'*URSUS ARCTOS* L. NOUVEAU-NÉ[2]

Le cerveau de l'*Ursus arctos* L. nouveau-né est remarquable 1° par son très petit volume, en rapport avec la très petite taille de l'animal, 2° par sa lissencéphalie à peu près complète.

[1] G. Elliot Smith, *Loco citato*, pp. 280 et 281.

[2] Pour la figuration voir R. Anthony et F. Coupin, "Le cerveau de l'Ours nouveau-né," *Loco citato*.

1°. *Rhinencéphale*

La topographie du rhinencéphale n'est, chez l'Ours à la naissance, indiquée que dans ses grandes lignes. La rhinale antérieure est bien visible, mais la rhinale postérieure n'est marquée qu'en avant.

L'endorhinale est bien accusée, mais le faible sillon qui sépare chez l'adulte le tractus olfactorius lateralis du gyrus du même nom est encore inexistant. Des sillons radiés que l'on observe chez l'adulte à la surface du gyrus olfactorius lateralis, seul celui qui paraît correspondre à l'incisura olfactoria est visible à la naissance, et, encore, sa présence n'est-elle pas constante.

Le gyrus ambiens est complètement lisse.

Le sillon limite postérieur du tractus olfactorius mesialis à la marge de l'hémisphère (sillon parolfactif postérieur—incisura prima de His) est très nettement visible.

Le tubercule olfactif est très bien circonscrit, mais sa surface est encore lisse.

Le lemniscus diagonalis Broca est volumineux, occupant tout l'espace perforé antérieur, mais il est mal limité. On n'observe encore aucune indication du gyrus lunaris, ni du gyrus intermedius.

La fissure hippocampienne est très nette et très profonde jusqu'au niveau postérieur du corps calleux; interrompue en ce point, de même que chez l'adulte, elle reparaît bientôt pour se continuer à la face supérieure du corps calleux limitant un hippocampe supracalleux qui s'atrophie de plus en plus chez l'adulte. L'interruption de la fissure hippocampienne correspond au gyrus Andreae Retzii qui est encore très étroit et mal limité.

La fissure fimbrio-dentée n'est encore marquée que dans sa région postérieure et inférieure.

Le gyrus dentatus, substance grise, qui, en raison de la non-indication à ce niveau de la fissure fimbrio-dentée, est macroscopiquement confondu en bas et dans sa région moyenne avec la fimbria (substance blanche), ne présente nulle part de denticulations.

Le gyrus fasciolaris, le gyrus intralimbicus ne sont pas macroscopiquement visibles; le gyrus transversus areae piriformis n'est pas encore indiqué.

Dans l'ensemble, le rhinencéphale est plus développé à ce moment que ne l'est le néopallium: il semble être à peu près au même état de développement que chez les autres Carnassiers au moment de la naissance.

2°. *Néopallium*

Le néopallium est à la naissance complètement lisse. Le seul plissement, peu net d'ailleurs, qu'on distingue à sa surface paraît correspondre à la calcarine.

D'autre part, on observe à sa face externe deux obscures dépressions: l'une qui correspond à la partie du territoire central qui sera operculisée plus tard, l'autre à la région située en avant de la présylvia. Sur la face interne, une

dépression située à la marge postérieure de l'hémisphère indique la place qui correspond à l'extrémité de la rhinale postérieure et au sulcus ursinus.

Les ébauches du lobe temporal et du lobe occipital sont encore peu marquées.

Le cerveau de l'*Ursus maritimus* Desm. nouveau-né est exactement dans le même état de développement que celui de l'*Ursus arctos* L. au même moment.

Cette lissencéphalie néopalléale à peu près totale des Ours brun et blanc à la naissance s'oppose à la grande gyrencéphalie des Canidés et des Félidés, même de petite taille, qui, à ce même moment, possèdent déjà leurs plissements fondamentaux. Elle est étroitement liée au faible volume du cerveau.

En résumé, le cerveau de l'*Ursus arctos* L., et aussi de l'*Ursus maritimus* Desm., est à la naissance dans l'état que présente celui des Carnassiers de moindre taille (le chat domestique et le chien par exemple) au tiers environ de la gestation.

III. LE DÉVELOPPEMENT DU CERVEAU DE L'*URSUS ARCTOS* L. APRÈS LA NAISSANCE

a. Le cerveau de l'individu âgé de 20 jours [voir figs. 1, 2, 3, 4, et 7 (*d*)]

1°. *Rhinencéphale*

Les principales modifications subies par le rhinencéphale de l'Ours brun de la naissance au vingtième jour sont les suivantes:

1°. La scissure rhinale postérieure s'étend maintenant jusqu'au bord postérieur de l'hémisphère, mais elle ne le dépasse pas ne se prolongeant encore sur la face postérieure.

2°. De très légers débuts de sillons radiés s'observent à la surface du gyrus olfactorius lateralis.

3°. Un début également de très légers sillons se montre sur le gyrus ambiens.

Le gyrus transversus areae piriformis n'a point encore fait son apparition, et, il en est de même du léger sillon qui sépare chez l'adulte le tractus olfactorius lateralis du gyrus du même nom.

Le rhinencéphale limbique ne présente pas de modifications importantes; le gyrus dentatus notamment est encore dépourvu de toute denticulation.

2°. *Néopallium*

Le néopallium, par contre, a beaucoup changé.

La suprasylvia est bien développée. Ce doit être le sillon qui, chez les Ours comme ailleurs, s'accuse le premier. R. Anthony et F. Coupin[1] ont, en effet, signalé sur un *Ursus thibetanus* Cuv. (No. 1896—89, ♀) à la naissance[2] l'existence

[1] R. Anthony et F. Coupin, "Le cerveau de l'Ours nouveau-né," *Loco citato.*

[2] Le cerveau de l'*Ursus thibetanus* Cuv. est, à la naissance, plus développé que celui de l'Ours brun et de l'Ours blanc. Ceci tient peut-être au moindre volume somatique de l'animal.

d'un seul sillon à la face externe de l'hémisphère et qui semble bien devoir être interprété comme la branche antérieure d'une suprasylvia.

L'ectosylvia est aussi bien développée, sa lèvre supérieure surplombant déjà considérablement la circonvolution I de Leuret. Il existe donc au vingtième jour un début très net d'operculisation, mais la fosse sylvienne est largement ouverte. C'est par le fait de l'accentuation de la flexion télencéphalique et du recourbement en avant du lobe temporal qu'elle se fermera plus tard.

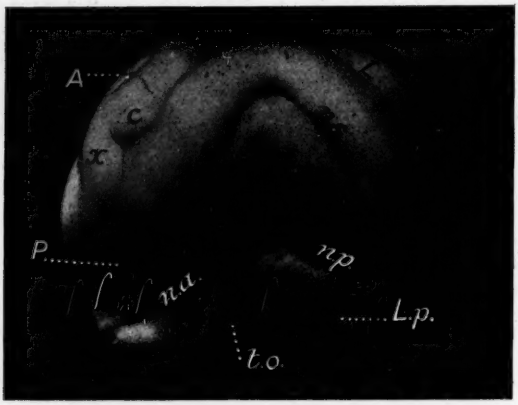

Fig. 1. Cerveau d'*Ursus arctos* L. (No. 1921—4, ♂), âgé de 20 jours. Face latérale externe gauche. Double de G. N.

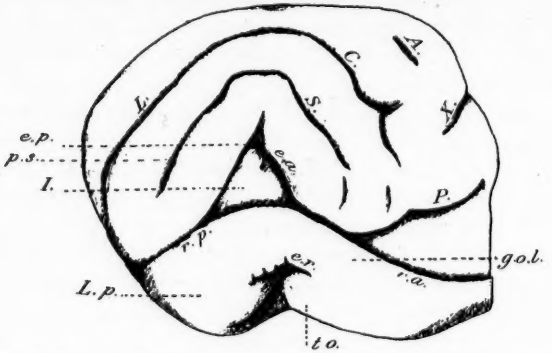

Fig. 2. Cerveau d'*Ursus arctos* L. (No. 1921—4, ♂), âgé de 20 jours. Face latérale externe droite. Double de G. N.

La pseudosylvia n'existe pas à droite, mais on voit très nettement à gauche l'indication de sa partie inférieure.

La présylvia est bien accusée. Il en est de même du corono-latéral qui se montre d'une seule venue dans les deux hémisphères.

Il existe, des deux côtés, un crucial déjà long et bien accusé, mais n'at-

teignant pas le bord marginal, une ébauche d'ansatus, à droite une ébauche d'ento-latéral, à gauche une ébauche de vertical.

L'orbitaire, le précrucial, les paracaudaux, le bissector n'ont point encore fait leur apparition.

Fig. 3. Cerveau d'*Ursus arctos* L. (No. 1921—4, ♂), âgé de 20 jours. Face inférieure. Double de G. N.

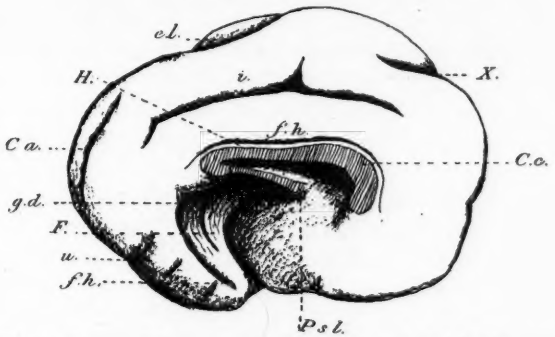

Fig. 4. Cerveau d'*Ursus arctos* L. (No. 1921—4, ♂), âgé de 20 jours. Face latérale interne gauche. Double de G. N.

Sur la face mésiale, la calcarine déjà indiquée à la naissance reste limitée à sa partie supérieure, et, il n'existe pas encore de paracalcarine.

L'ursinus, dont la place était déjà marquée à la naissance, s'est indiquée nettement.

L'intercalaire est profondément indiqué à gauche, mais il n'est représenté à droite que par des sillons courts, peu profonds et indépendants les uns des autres.

β. Le cerveau de l'individu âgé de 22 jours (voir figs. 5 et 6)

1°. *Rhinencéphale*

Les principaux changements intervenus dans le rhinencéphale entre le 20ème et le 22ème jours sont les suivants:

1°. Accentuation plus grande des sillons radiaires du gyrus olfactorius lateralis.

2°. Indication du léger sillon qui sépare le tractus olfactorius lateralis du gyrus du même nom.

3°. Réduction déjà perceptible de l'hippocampe supracalleux.

La fimbria, le gyrus dentatus, le crochet de l'hippocampe n'ont pu être étudiés en raison du mauvais état de conservation de la pièce.

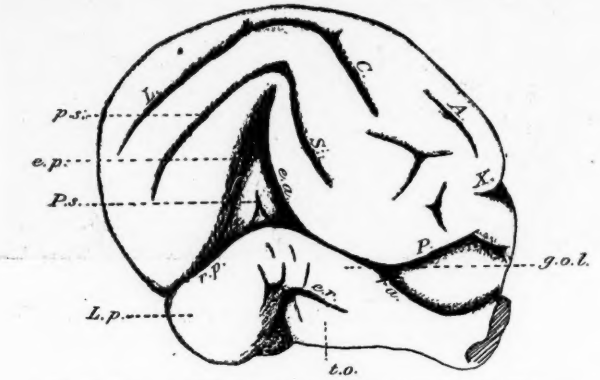

Fig. 5. Cerveau d'*Ursus arctos* L. (1921—4, ♀), âgée de 22 jours. Face latérale externe droite. Double de G. N.

2°. *Néopallium*

L'aspect du néopallium à 22 jours est peu différent de celui qu'il présente à 20 jours.

1°. Les principaux faits à signaler sont les suivants:

2°. Extension de l'ébauche de l'ansatus aussi bien à droite qu'à gauche.

3°. Très légère ébauche de précrucial à gauche.

L'intercalaire est nettement accusé des deux côtés.

CONSIDÉRATIONS GÉNÉRALES

L'ordre de développement des sillons néopalléaux ne semble pas être différent chez les Ours de ce qu'il est chez les autres Carnassiers.

Si l'on prend comme type le Chat domestique dont le développement cérébral est assez bien connu[1], on constate par exemple que chez un embryon de 8 cm. (R. Anthony) le seul sillon qui existe à la surface externe du néopallium est la scissure rhinale dont on ne voit encore à ce moment que la

[1] Voir par exemple P. Martin, "Zur Entwickelung der Gehirnfurchen bei Katzen und Rind," *Arch. f. Wiss. u. prakt. Tierheilk.* 1895.

partie antérieure. C'est exactement ce que l'on constate chez l'Ours brun, comme d'ailleurs chez l'Ours blanc, à la naissance.

Ce mode de développement des rhinales paraît être général; on l'observe très nettement aussi chez l'embryon humain au cours de la deuxième moitié du 3ème mois.

De même, chez un embryon de chat de 11 cm. (P. Martin), il existe, outre les rhinales, la branche antérieure de la suprasylvia, la présylvia, la branche

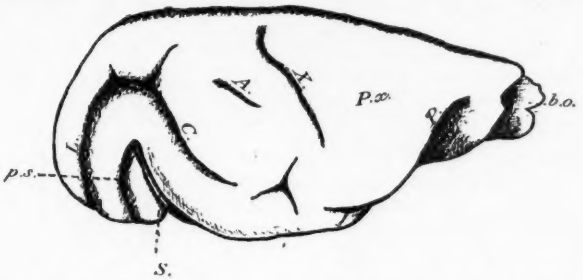

Fig. 6. Hémisphère droit d'*Ursus arctos* L. (No. 1921—5, ♀), âgée de 22 jours. Face supérieure. Double de G. N.

antérieure de l'ectosylvia, le coronal, le latéral et l'ébauche inférieure de la pseudosylvia. On voit par là que, chez le Chat comme chez les Ours, la suprasylvia se développe d'abord par sa partie antérieure (*Ursus thibetanus* Cuv. No. 1896—89) et la pseudosylvia par sa partie inférieure (voir figs. 1 et 5).

Ce n'est que chez un embryon de chat de 12 cm. (P. Martin) que la branche postérieure de l'ectosylvia commence à apparaître.

Sur la face mésiale d'un cerveau de foetus de chat de 8 cm. (R. Anthony), on constate aussi, comme chez l'Ours, la précocité des ébauches du splénial et de ses parties constitutives (calcarine-intercalaire-rostral).

Si, du néopallium, on passe au rhinencéphale on peut mentionner, chez le Chat comme chez l'Ours, la précocité de développement de l'incisura olfactoria et la grande importance que présente au cours de la vie embryonnaire l'hippocampe supracalleux.

La marche du développement est donc la même dans les deux espèces, mais, ce qu'il faut retenir, c'est le retard considérable que présente chez les Ours, par rapport aux autres Carnassiers, le développement télencéphalique.

L'aspect du cerveau de l'Ours est à la naissance celui d'un cerveau d'embryon de chat de 8 cm., et, l'aspect d'un cerveau de chat nouveau-né correspondrait à celui d'un cerveau d'Ours de plus de 20 jours.

L'établissement de ces deux points constitue le principal intérêt particulier de cette étude; mais, en se plaçant à un point de vue plus général, celle-ci montre encore comment, chez les Ursidés, s'établit le recouvrement de la circonvolution I par la circonvolution II, comment se constitue le complexe

sylvien, comment en un mot se fait l'operculisation d'une partie du territoire central.

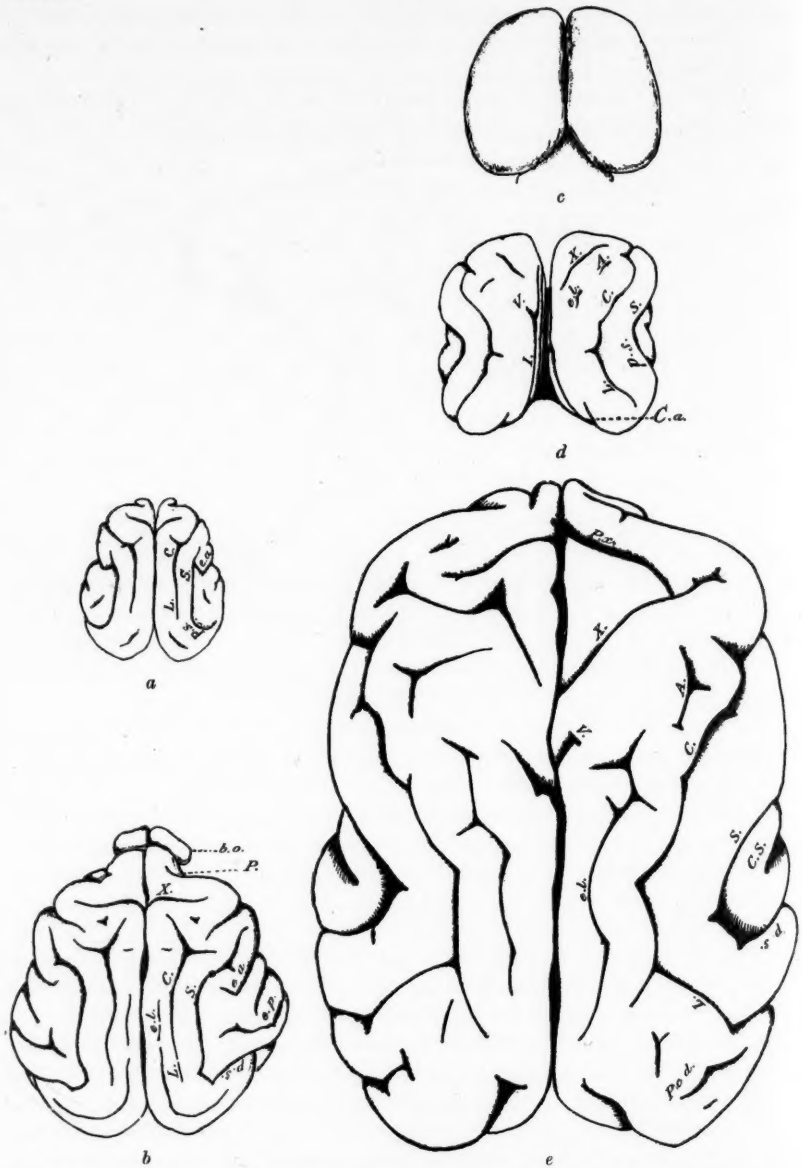

Fig. 7. A gauche, cerveaux de chat domestique. De haut en bas: *a*, cerveau de nouveau-né; *b*, cerveau d'adulte. A droite, cerveaux d'*Ursus arctos* L. De haut en bas; *c*, cerveau du nouveau-né (1919—8, ♀); *d*, cerveau de l'individu âgé de 20 jours (1921—4, ♂); *e*, cerveau de l'adulte (1911—216, ♂). Faces supérieures. G. N.

Nos observations qu'il y aurait sans doute lieu de compléter et d'essayer d'étendre aux Mustélidés et aux Pinnipèdes viennent ainsi appuyer d'un argument embryologique l'interprétation que les travaux de W. Turner, G. Elliot Smith, Holl, R. Anthony et Santa-Maria ont donné de la morphologie néopalléale des Mammifères.

SIGNIFICATION DES LETTRES EMPLOYÉES DANS LES FIGURES

1°. *Rhinencéphale*

r.a. (*n.a.* dans figs. 1 et 3) = rhinale antérieure; *r.p.* (*n.p.* dans figs. 1 et 3) = rhinale postérieure; *g.o.l.* = gyrus olfactorius lateralis; *e.r.* (*e.n.* dans fig. 3) = endorhinale; *t.o.* = tuberculum olfactorium; *l.p.* = lobe piriforme; *i.o.* = incisura olfactoria; *H.* = hippocampe; *f.h.* = fissura hippocampi; *g.d.* = gyrus dentatus; *F.* = fornix; *Psl.* = psaltérium.

2°. *Néopallium*

S. = suprasylvia; *p.s.* = postsylvia; *e.a.* = ectosylvia antérieure; *e.p.* = ectosylvia postérieure; *C.S.* = complexe sylvien; *C.* = coronal; *L.* = latéral; *X.* = crucial; *P.x.* = précrucial; *A.* = ansatus; *P.* = présylvia; *I.* = Gyrus I; *P.s.* = pseudosylvia; *e.l.* = ento-latéral; *Ca.* = calcarine; *i.* = intercalaire; *u.* = ursinus; *V.* = vertical; *Pcd.* = paracaudaux; *C.c.* = corps calleux.

FUSION OF CARPAL ELEMENTS

By A. J. E. CAVE, M.B., Ch.B., F.Z.S.
(*Anatomy Department, University of Leeds*)

Whilst numerical increase of the carpal elements, by the occurrence of the os centrale, os styloideum carpi, etc., is by no means uncommon, the opposite condition—genuine non-pathological reduction in number of the carpalia—is relatively rare. Such reduction, when it occurs, is due to the early fusion, or the non-separation of two of the normal wrist bones. Thus Turner (1) has described the trapezium and scaphoid forming a single bony piece, and several cases of fusion of the semilunar with the cuneiform, recorded by various authors, have been summarised by S. A. Smith (2) in a previous volume of this *Journal*. Gougerot (3) makes mention of a case of absence of the fifth digit, where the carpus presented fusion of a rudimentary unciform with the os magnum and fusion of the semilunar with the trapezium. In 1883 Anderson (4) described a union of the os magnum and trapezoid in a right upper extremity

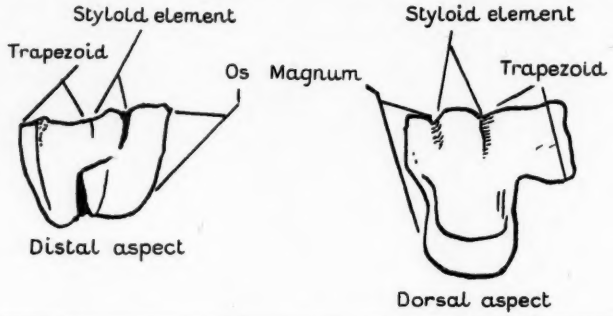

Fig. 1. Left anomalous bony piece, distal and dorsal aspects.

possessing no other unusual features, a case similar to the one now to be presented.

The latter consists of the fusion of the os magnum and trapezoid in both wrists of an adult male subject from the Leeds University dissecting room, in whom no other osseous anomalies of any note were discovered. Both wrists were free from any signs of disease (tuberculous or otherwise), and careful examination of the anomalous pieces (including section of one of them) failed to reveal any sign of joint cavity, or of any previous fracture.

The diagram represents the dorsal and distal aspects of the conjoined bones of the left wrist, their appearance being somewhat complicated by the presence

of the styloid apophysis of the third metacarpal bone; for this ossicle, detached from its normal site, is incorporated in the fused mass of the magnum and trapezoid. On its proximal and dorsal surfaces the anomalous bony piece shows no trace of division, but the distal aspect exhibits a groove, extending slightly palmarwards, which indicates the dual nature and origin of the bone.

The standard anatomical authors consulted do not refer to fusion of the os magnum and trapezoid—a condition which would appear to be rare—nor have I been able, so far, to find a similar case in the radiological literature at my disposal. In the lower mammals the Carnivora usually have the scaphoid and semilunar fused; the little anteater (*Cycloturus didactylus*) has the magnum, trapezoid and unciform confluent; the three-toed sloth (*Bradypus tridactylus*) exhibits fusion of the magnum and trapezoid—though these bones are distinct in *Choloepus*—and a fusion of the same carpalia is to be found in certain Pecora, and in some species of Tragulina, including *Leptomeryx* from the North American Miocene.

It is obvious that no inference can be drawn from the occurrence of a fusion in the human carpus corresponding to that found in the carpi of such diverse and highly specialised forms. Investigation(5) has shown that the styloid apophysis remains independent of the third metacarpal in over 5 per cent. of cases, being fused with the magnum in 3 per cent. of cases and with the trapezoid in 0·4 per cent. of cases; it is suggested that in the present case the detached styloid ossicle is responsible for the welding together of the magnum and trapezoid, at least in part.

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REVIEW

Dentition and Palate of the Australian Aboriginal. By T. D. Campbell, D.Sc., University of Adelaide: Publications under the Keith Sheridan Foundation, No. 1 (Adelaide: The Hassell Press), 1925, pp. 123. Plate LIII. Price unstated.

This monograph represents the thesis presented by the author for the degree of Doctor of Dental Science in the University of Adelaide. By its publication anthropologists have placed at their disposal for the first time an adequate description, with full data, of the teeth, palate and jaws of Australian aborigines. Dr Campbell was able to examine in the museums of Australia 630 dentitions more or less complete, 340 of his examples being drawn from South Australia. His monograph in its method, scope, statement and exhaustiveness is a model which other workers will do well to copy.

The various subjects dealt with are the following: four measurements of each tooth are given; the medio-distal, the labio-lingual, height of crown, length of root, and the means of measurements thus obtained are compared with similar measurements of the teeth of Europeans and of Japanese. The Australian measurements exceed those of other races by considerable amounts. Cusp development and root development are then dealt with; the variability of each tooth is considered, the third molars being the most variable, the upper central incisors the least. Dr Campbell found that 99·8 of the full complement of wisdom teeth were present in the jaws of Australian aborigines whereas in European dentitions only 70 to 80 per cent. of the full complement is attained. On the other hand 1·5 per cent. of skulls showed a supplemental or fourth molar. Crowding of the teeth is rare; the palate of which the mean dimensions are given, is well expanded and developed. Dr Campbell found that with the eruption of the permanent premolars there was a widening of the palate amounting in the average to 9 mm. A full account is given of the order of eruption. The extra cusp, known as Carabelli's cusp, is three times more common in the molars of Europeans than in those of the Australian aborigines. One very interesting fact is brought out, namely, that for some time after the eruption of the permanent incisors the bite is of the overlapping type; it is only later that the edge-to-edge bite is attained. Specially valuable is the description of the nature of the articulation or contact of the lower molars with the upper. The degrees of prognathism, the form of the glenoid fossa, attrition, caries (the second molars are the most frequently affected), dental abscess, food, mastication, and mutilation have been investigated and described. Dr Campbell has contrasted the palate and dentition of the Australian aborigines with those of fossil types of mankind. It will be seen that this monograph supplies anatomists, anthropologists and dentists with data they stand much in need of and supplies them in a most acceptable form.

A. K.

Anatomical Society of Great Britain and Ireland

PROCEEDINGS

July, 1925 *November*, 1925
February, 1926

RECORDED BY
R. J. GLADSTONE

EDITED BY
E. BARCLAY-SMITH

PROCEEDINGS OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND

JULY 1925

THE Summer Meeting of the Society was held at King's College, London, on Friday, July 3rd, and in the Rooms of the Zoological Society of London on Saturday, July 4th, 1925, the President, Professor G. ELLIOT SMITH in the Chair.

(1) Professor HILL and Mr SUBBA RAU gave a brief account of a collection of pregnant uteri of *Loris gracilis*, recently received through the kindness of Dr Kuni Kanan, Mysore State, S. India. They exhibited lantern slides showing a four-celled egg in the Fallopian tube, as well as other slides illustrating the arrangement of the foetal membranes and the structure of the placenta. In its placentation, *Loris* closely resembles the other Lorisiformes, *Nycticebus* and *Galago*, the diffusely arranged chorionic villi having the form of short columns, more or less polygonal in cross section, which fit into corresponding crypts in the uterine mucous membrane. Chorionic vesicles are present but are less richly provided with internally projecting villi than are those of the other two genera mentioned. Contrary to the usual statement in books, twins in this species appear to be not uncommon.

(2) Professor ELLIOT SMITH communicated an extract of a paper by Dr H. H. Woollard, on "The Retina of *Tarsius*, and the Evolution of the macula lutea."

(3) Miss UNA FIELDING made a preliminary communication on "The Brain of *Notoryctes typhlops*." The material used for the investigation was a series of transverse sections of the cerebral hemisphere and diencephalon of *Notoryctes typhlops*, stained with carmine—the property of Prof. G. Elliot Smith.

The brain of *Notoryctes typhlops*, the blind marsupial mole of Australia, is, with the possible exception of that of *Caenolestes obscurus*, the small shrew-like S. American marsupial, the most generalised of all mammalian brains. It offers excellent opportunities for working out homologies with the brains of Reptiles on the one hand, and the higher Mammals on the other. The principal feature of the present communication is the analysis of the amygdaloid complex. The lamination of the cerebral cortex and the changes in the mid-brain consequent upon the lack of optic inflow will be described at a later date.

Amygdaloid Complex. Drawings of ten transverse sections were shown. Five different cell groups are distinguishable, viz.: Basal, Cortical, Medial, Central and Lateral Amygdaloid Nuclei.

[Note. This terminology is that of J. B. Johnston, used in his work on the amygdaloid nuclei of the Virginia opossum, *Journ. Compar. Neurol.* Aug. 1923.]

No accessory basal amygdaloid nucleus (Johnston) was found in *Notoryctes*.

A very large stria terminalis is present having its connections posteriorly with the medial and central amygdaloid nuclei and so far as can be judged from the material at present available with the basal and lateral nuclei also.

Rising dorsal to the crus the stria terminalis passes to the hypothalamus.

No bundle of the stria terminalis has as yet been seen passing dorsal to the anterior commissure. Further connections of the stria terminalis and other fibre tracts related to the amygdaloid nuclei will be described when serial sections specially stained for fibres are available.

(4) Dr S. POLJAK read papers on

(A) "The Connections of the Acoustic Nerve."

The organisation and function of the auditory system of Mammals provide one of the most obscure chapters of the anatomy of the nervous system. This obscurity is mainly due to the long course in the brain stem and to the fact that the auditory path consists of a chain of differently linked neurones.

The present investigation was begun by a careful examination of the whole auditory system (ramus cochlearis and its central connections) of the small insectivorous bats of South Europe—*Pterygistes noctula* and *Rhinolophus ferrum-equinum*. These animals have a highly specialised mode of life and depend on one kind of food only, namely nocturnal insects. In accordance with their mode of life the senses of touch and hearing are enormously developed, while the other senses, more particularly the organs of sight, are proportionately reduced. It was hoped that the great development of the structures associated with the sense of hearing in these animals would facilitate the solution of some of the anatomical and physiological problems of audition.

The method of investigation consisted of the study of serial sections stained with toluidin blue, Van Gieson, Weigert and a series stained by the Marchi method after injury of the cochlear ganglion. In addition a large number of Golgi impregnations of the embryos of rats, mice and cats were studied. Finally Weigert series of the brain stems of monkey and of man were studied. In order to localise in the brain stem the level of the various acoustic reflexes, experiments consisting of complete transverse, sagittal and partial transverse sections were made on the brain stem of rats and cats.

The results of these investigations may be summarised as follows:

I. Special characteristics of the acoustic system of the small bats (Microchiroptera).

The ramus cochlearis is relatively very large and much larger than the ramus vestibularis. On the other hand the size of the cells composing the ganglion spirale is only about one half the size of the cells composing the vestibular ganglion (ganglion Scarpae). Both nerves are extremely short and the bundles composing the cochlear nerve lose their sheath of Schwann while still within the modiolus.

The point at which the sheath disappears varies slightly for the different bundles.

The excessively large primary cochlear centres are quite extramedullary and begin at the base of the modiolus. They consist of three parts—the dorsal cochlear nucleus (the tuberculum acusticum), the oral and the caudal portion of the ventral cochlear nucleus. The last two are almost completely separated from each other by the entering bundles of the cochlear nerve.

The superficial cells of the dorsal nucleus show a tendency to form groups. The oral part of the ventral nucleus is composed of cells scattered uniformly, while the caudal part consists of a thick plate of nerve cells and fibres forming three folds or gyri. The dorsal and the ventral folds are small and their concavities are directed towards the lateral side, while the larger middle fold has

its concavity directed toward the medial side, to the beginning of the corpus trapezoideum. The cells are small in the dorsal and the ventral gyri, large and spindle-shaped in the middle gyrus. The secondary auditory ganglia (the nucleus olivaris superior principalis, n.o.s. accessorius and the nucleus trapezoideus with their satellite cell agglomerations) show the same excessive size. In the region where they are best developed they occupy, in transverse section, the ventral half of the brain stem, extending from the corpus trapezoideum and spinal root of the Vth nerve laterally to the raphe medially. The largest cells are found in the accessory olive, the smallest in the main superior olive (principalis). Both the olives are continued into the tertiary centre, the inferior lemniscal nucleus. There is however a marked difference in the cells. They are smaller in the lemniscal nucleus than in the accessory olive and being more condensed form a more uniform mass. The dorsal portion of the lemniscal nucleus is dispersed into a number of small cell islets containing also some fusiform transversally placed cell elements.

In accordance with the high development of the lower internodes of the acoustic system the posterior quadrigeminal body is also of large size. It consists of a central nucleus composed of a large number of small and middle sized elements surrounded by cells of larger size forming an annular formation. The latter surpass in size the large cells of the reticular formation. In the oral portion of the posterior quadrigeminal body these large cells are continued into the efferent portion of the anterior colliculus, the multipolar cells of which exceed in size those of the ventral horn cells of the cervical intumescence of the cord—nucleus motorius tecti intratrigeminalis of Kohnstamm-Quensel.

The lateral portion of the posterior quadrigeminal body shows a well-defined stratification. The afferent part of the anterior colliculus shows a striking contrast to the posterior colliculus and to its own motor portion, being for the most part reduced and composed of a few atrophied nerve cells.

The medial geniculate body is large and greatly exceeds in size the almost non-existent lateral geniculate body. It is however much smaller than the posterior quadrigeminal body and shows well-marked cell stratification.

In the oculo-motor apparatus it is not possible to verify the existence of an abducens nerve and nucleus. The third and the fourth exist as small and little differentiated cell groups. The uncrossed tectopontine fascicle from the posterior colliculus ends in an exceedingly well-developed lateral pontine nucleus.

The investigations of the fibre connections show, as the most important fact, that the oral part of the ventral cochlear nucleus sends its fibres of fine calibre exclusively to the homo-lateral superior olive as the dorsal non-crossing portion of the corpus trapezoideum and also to the retro-olivary substance and probably to the inferior lemniscal and paralemniscal nuclei of the same side.

The caudal laminated portion of the ventral cochlear nucleus on the contrary consists of coarse fibres which are mainly connected with the trapezoid nucleus and probably with the superior olive of the opposite side. In addition it contains a moderate number of fine ascending fibres which pass to the secondary ganglia of the same side.

The most important result of a study of the Golgi impregnations is that both superior olives receive fibres from the corpus trapezoideum of both sides. These terminate in the same olivary elements as was shown by Cajal for the laminary nucleus of birds. Most of the axis cylinders arising from the olives

and all those arising from the nucleus trapezoideus take a lateral direction and probably form in part the lateral lemniscus. Some of the fibres arising from the retro-olivary cells cross the median raphe, others end in the dorsal reticular formation of the same side.

The results of the experiments showed that most of the acoustic reflexes, particularly those of a general character, e.g. lifting of the head, activation of the entire musculature of the body and the extremities, simple ear movements, but not lateral movements of the head, or the precise movements of the ear are performed by brain stem mechanisms lying behind the midbrain. They are performed by the medulla oblongata and the pons—that is, they are executed by the secondary acoustic ganglia, the surrounding reticular substance, and by the lemniscal and paralemniscal nuclei. Delicate movements, lateral movements of the head and rotation of the pinna are very probably executed by the inferior colliculus.

In general it may be said of the Microcheiroptera that they exhibit a marked dominance of the sense of hearing. It remains to be shown whether the tactile sense in these animals exhibits a similar dominance over the other senses. It is interesting to observe that this dominance of one particular sense was imposed by the manner of living and at the same time reduced the other senses, with the exception of tactile sense, almost to a vestigial condition.

II. Taking into account the results of other investigators as well as the present investigations the following scheme of the mammalian acoustic system may be justified. The statements not fully proven appear in parentheses.

Each of the bipolar cells of the spiral ganglion gives off a peripheral fibre to the organ of Corti and a central fibre (the ramus cochlearis of the VIIIth nerve) to the primary acoustic centres of the brain stem. Here the central fibre divides into two branches, an anterior terminating in the oral portion of the ventral cochlear nucleus and a posterior terminating in the caudal portion of the same nucleus and in the dorsal cochlear nucleus—tuberculum acusticum.

There are three divisions of the primary acoustic centres and they are the starting-point of three different, but not completely isolated, central systems.

The first path arises mainly from the dorsal nucleus (possibly receives a small number of fibres from the caudal part of the ventral nucleus). These form the so-called dorsal acoustic path (Held and Monakow) and go to the superior olive of the same and opposite sides. A few fibres may join the lateral lemniscus of the opposite side, forming its medial portion, and finally reach the opposite inferior colliculus.

The second and the third paths form the so-called ventral acoustic path (Flechsig), the corpus trapezoideum. The second arises from the medium-sized cells in the oral portion of the ventral cochlear nucleus and is entirely homolateral, forming the dorsal and more oral portion of the trapezoid body. It consists for the most part of fine fibres terminating in both portions of the homolateral superior olive, in the surrounding reticular substance (and probably in the lemniscal and paralemniscal nuclei) of the same side.

From the "complex of the superior olive" some fibres reach the abducens of the same side—the real olivary peduncle. (Others go to the opposite oculomotor nuclei.) Most fibres however take a lateral direction and very probably become incorporated in the lateral fillet of the same (and opposite) side, going to the inferior colliculi. (Nothing can be said about fibres passing in a spinal direction.)

The third path springs from the large cells of the caudal laminated portion of the ventral nucleus and is for the most part crossed. It contributes fibres to the ventral and more caudal portion of the trapezoid body. These consist of the coarse fibres passing to the trapezoid nucleus and the superior olive of the opposite side. Further by means of direct collateral fibres it is in connection with the reticular substance of both sides and forms finally the lateral part of the crossed lateral fillet. (The existence of direct cochlear root fibres to the opposite trapezoid nucleus needs further confirmation.)

The crossed fibres from the first and the third paths make connection with the opposite (and by direct non-crossed fibres partly with the homolateral) lemniscal nuclei and the pontine reticular substance.

The superior olive, chiefly the principal lateral portion, constitutes a partial junction of the secondary auditory paths of both sides.

The lateral fillet contains functionally heterogeneous components: (*a*) crossed secondary fibres; (*b*) crossed fibres interrupted in the opposite trapezoid nucleus, therefore tertiary components running to the lemniscal nuclei and to the inferior colliculus; (*c*) combined bilateral tertiary fibres interrupted in the superior olive (and possibly (*d*) a small number of non-crossed secondary fibres to the tectum).

The lemniscal fibres reach the inferior colliculus (possibly also in a direct course the superior colliculus, the motor apparatus of the mid-brain and the medial geniculate body). Here arises a tertiary acoustic path, combined with the medial geniculate body, the last interruption before entering the neopallium. In such manner both halves of the brain stem and both hemispheres receive stimuli from each peripheral receptive organ (the crossed connections, however, predominate).

The constituent parts of the central auditory system have mostly a double function—viz. to conduct the peripheral auditory sensations to the prosencephalon on the one hand, and on the other, to establish a reflex path for the cochlear stimuli to the motor mechanisms of the brain stem. (The trapezoid nucleus and its conducting system and also partly the lemniscal and paralemniscal nuclei are probably prevailingly motor.)

All the links of the acoustic system beginning with the peripheral organ of reception and including the primary cortical centres of hearing are entirely or for the most part organised in such a way as to render possible the perception and the conduction of qualitatively different peripheral stimuli (and the ultimate utilisation of them by the brain stem and the fore-brain).

According to the quality of the stimulus perceived by the organ of hearing and the character of the latter as a tele-receptor the motor function of the auditory system is to perform movements of vital importance, e.g. avoidance of danger, acquisition of food, and the facilitation of reproduction. The acoustic reflexes underlying these functions are all carried out by the brain stem. (About those involving the fore-brain nothing is known.) Reflexes which are of a more general character involving the activation of the whole somatic neuromuscular system, and partly vegetative, are performed by the lower half of the brain stem, the medulla oblongata and the pons. Reflexes which involve a more specific response, e.g. a better orientation in space, are carried out by the mid-brain. The efferent portion of the latter part of the cochleo-motor apparatus is not a separate system. It subserves moreover for the same purpose, the impulses coming from the other organs of sense (optic, tactile, etc.).

It stands in anatomical and physiological connection with the lateral pontine nuclei and the cerebellum.

(B) "Association Fibres of the Cerebral Cortex."

As, in recent times, some doubts have been thrown on the existence of the long intrahemispherical fibres of the human and mammalian brain (Niessl von Mayendorf, *Arch. f. Anat. u. Phys.* 1919) it was considered advisable to attempt the solution of this problem, at least in principle, by the method of inducing lesions of isolated portions of the cortex and following the degeneration of the fibres by the Marchi method.

The first examinations by this method were carried out on the cat. The visual receptive area of this animal was chosen since from the researches of Brodmann and Minkowsky its extent is tolerably certain. The visual area, being easily accessible was removed entirely in its antero-posterior extent and for about half its transverse extent. The destruction was confined to the cortex. This was confirmed by microscopic examination and at the same time injury or inflammation of neighbouring areas not belonging to the primary visuo-receptive territory was excluded.

The microscopic examination of the brain so operated on and stained led to the following conclusions:

There are three fibre systems arising in the area striata:

1. Fibres going to the corpus callosum.

2. Fibres passing through the white matter in the stratum sagittale internum to the diencephalon and mesencephalon ending there only in the superior colliculus. A very few fibres end in the stratum zonale and in the stratum griseum superficiale of this body; the majority end in the stratum medullare superficiale.

3. Fibres terminating in the different cortical regions of the same hemisphere. These may be subdivided into:

(*a*) Short U-shaped fibres (Arnold-Meynert) running to the immediately adjacent gyri splenialis, suprasylvius and supraplenialis (*vide* atlas of Winkler-Potter, 1914).

(*b*) Long association fibres, quite distinct from the preceding, passing directly to the mid-portions of the middle and posterior ectosylvian gyri.

No evidence of the existence of other long-fibre systems passing to other cortical areas, as for instance the Rolandic area, was found. It is of interest to draw attention to the fact that the areas so related to the primary visual zone are situated midway between this area and the primary cortical acoustic centre. Since the cortical area between the two is not directly joined with either it may be regarded as the zone in which optic, auditory and probably tactile, etc., impulses are compounded together. In other words this area may be regarded as a primitive associational area (Flechsig).

The results obtained from the study of the brains of lower mammals cannot be directly transferred to man. However it is probable that a study of the primate brain from this point of view would give results of much greater significance for man.

(5) Dr A. Blackhall Morison exhibited specimens and read a paper on "The Innervation of the Cardiac Ventricle," a full account of which is published in the *Journal*, vol. lix, pt 2.

In the discussion which followed Sir Arthur Keith stated that in his

opinion the nerve supply of the muscular coats of the coronary vessels was sympathetic not vagal.

Professor HILL said that nerve ganglia were undoubtedly present in the proper ventricular muscle.

Dr WOOLLARD commented on the importance of employing selective stains for the demonstration of special nerve fibres. With the usual staining reagents to which heart tissue was subjected, only one type of nerve fibre was demonstrated.

Professor WATERSTON, said that Professor Bolk's specimens showed that the endings of the nerve fibres in cardiac muscle were hypolemmal. They terminated as fine fibres without medullated coat. The nerve fibres were singularly like those demonstrated by Kulchitsky in ordinary striated muscle.

(6) Professor K. KOSAKA read a paper on "The Effects of Ascending and Descending Electrical Currents on the Growth of Tissues and Nerves."

(7) Professor D. WATERSTON read a paper by Dr W. G. ROBERTSON and himself on "The Development of the Cranial Nerve Nuclei in the Human Embryo." The paper was illustrated by models and linear reconstructions of stages in the development of the cranial nerve nuclei in a series of human embryos.

In the discussion which followed Miss MANN expressed the opinion that the Edinger-Westphal nucleus is a later growth and that the nucleus which appears in the earlier embryos is probably a lateral outgrowth from the true third nucleus.

Dr LE GROS CLARK referred to the phylogenetic development of the IIIrd nerve. A fusion of the nuclei takes place. In *Tupaia* and *Lemur* the IIIrd nerve has two main lateral nuclei, and two detached groups of cells which are situated between these and the median plane and which appear to be derived from the lateral nuclei.

Professor FRAZER referred to the sulcus on the lateral wall of the third ventricle described by Professor Waterston, and said that he had been unable in his specimens to trace the sulcus limitans up to the third ventricle. In the mid-brain it was prolonged upwards on to the dorsal side.

The IVth cranial nerve made its appearance in the hind-brain on the caudal side of the isthmus.

Professor ARTHUR THOMSON considered that the evidence pointing to absence of neuromeres in this region was inconclusive.

Professor HILL said he had been unable to recognise the sulcus limitans in the earlier stages of development in lower Mammals, and that he did not consider its presence or absence of primary significance. With regard to the apparent lack of evidence of neuromeres in the models shown, he presumed that the authors did not wish to deny the existence of neuromeres in this region, since they are certainly present in all lower types.

Professor ELLIOT SMITH said that the Edinger-Westphal nucleus was very difficult to find in lower Vertebrates. In some there was no indication of its existence. In higher Mammals it was not developed until a late stage.

Professor Waterston, in reply, said that the description which he had given must be regarded as an accurate representation of the observations which had been made. There was an undoubted extension forward from the nucleus of the IIIrd nerve, but whether this was of regular occurrence was open to

question. A groove on the lateral wall of the third ventricle in the situation which he had described was undoubtedly present but whether it represented the sulcus limitans or not was open to question.

(8) Professor PATTEN demonstrated:

(A) A model showing unusual variations of the coeliac axis and superior mesenteric arteries.

An unusually large artery, with a diameter of 1·3 cm. at its origin, arose from the front of the abdominal aorta at the level of the 12th thoracic vertebra. This vessel extended obliquely forwards and to the right, and after a course of 2·5 cm. gave off a very small short axial trunk, measuring 7 mm. only in length. This vessel divided immediately and in a radial manner, into hepatic, duodenal, and gastric arteries. From the last mentioned a *very small* splenic artery took origin. This very short and very small axial trunk evidently represented the coeliac axis reduced in size and springing abnormally from the unusually large vessel above mentioned. The latter having given off this abnormally situated coeliac axis, was prolonged downwards vertically as the superior mesenteric, presenting the normal arrangement and distribution of its branches. A very interesting feature of the case was that the main supply of blood to the spleen was conveyed by a branch which took origin directly from the abdominal aorta. It was smaller than normal and exhibited little or no tortuosity, the characteristic feature of this vessel. This splenic artery sprang from the abdominal aorta about a centimetre above the left renal: the latter and also the right renal were normal in origin and mode of distribution. Immediately above the right renal another interesting variation was presented in the form of a second hepatic artery springing from the abdominal aorta directly. This vessel was somewhat smaller than one of the primary divisions of a hepatic artery of normal origin. It is to be noted that the splenic and hepatic arteries were duplicated at their origins; an extra branch in each case arising from the abdominal aorta. The part of this system of arteries which represented the distribution to the stomach and gut was, on the whole, somewhat more strongly developed than usual and arose by a common stem directly from the abdominal aorta: on the other hand, that part whose branches were distributed to the spleen and to the liver was less vigorously developed and arose only in part from the common stem, the remaining part being represented by duplicated arteries.

(B) A human cranium showing indications of divided parietals.

In a mesaticephalic cranium of a modern European type, with a cephalic index of 79·4, with metopic, lambdoid, squamo-parietal and the greater part of the coronal sutures still open, and with the sagittal suture for the greater part of its course occluded, two interesting markings were present, one on either parietal bone, which were suggestive of the presence of former anomalous sutures. On the right side the suture commenced 5 cm. below the bregma in the coronal suture, and extended backwards parallel to the sagittal suture until it reached a point 1·5 cm. from the lambdoid suture; it then curved downwards and joined the lambdoid suture at 5·6 cm. from the lambda. On the left side the anomalous suture is masked in its front part by an indentation on the skull 1·5 cm. in diameter which appears to have been a depressed fracture. The posterior segment of the suture extends horizontally backwards in a manner similar to that of the right side, but when within 1·8 cm. of the lambdoid

suture it curves downwards and ends in the asterion. While these parietal markings appear sufficiently pronounced to suggest persistent remnants of former complete sutures, they may, on the other hand, be excessively developed upper temporal lines and may have been associated therefore with the attachments of the upper limits of the temporal fasciae. The downward curving of the posterior parts of these parietal markings lends support to this view. Possibly however the line of subdivision of the parietals may have taken place in close correspondence with the site of the developing upper temporal lines. The marking on the right parietal (the more pronounced of the two) has, from its appearance, some claim to a sutural origin.

Professor WINGATE TODD commented on the remarkable tortuosity, which was frequently exhibited by the abdominal arteries, and the frequency of variations in the main vessels and their branches.

Referring to the frequency of divided parietals, he considered the condition must be rare, as in the examination of 2000 specimens, he had only met with one case.

(9) Dr GIRGIS demonstrated a wax model of the brain of a human embryo of 22 somites, a full description of which is published in the *Journal*.

Professor HILL commented on the small size of the fore-brain region of the human embryo at this stage of development as compared with that of lower Mammalia. The same feature was indicated in the reconstruction models of Peter Thompson and Hochstetter.

Dr Girgis also demonstrated the genital organs of a human hermaphrodite, a description of which was communicated to the Society at the Summer Meeting in 1922 by Professor Derry. The paper appears in the *Journal*, vol. LVII, pt 3.

(10) A paper was read by the late Dr C. F. SONNTAG, entitled "Notes on the Evolution of the Tongue."

The PRESIDENT drew attention to the value of the evidence supplied by details in the comparative anatomy of the tongue and their great importance as a means of checking or confirming conclusions drawn from a study of other regions of the body.

(11) Professor T. WINGATE TODD read papers on

(A) "The Yearly Fluctuation in the Cranial Capacity of a Dissecting Room Population."

A dissecting room population is clearly made up of social ineffectives. The average cranial capacity of our male white material has varied considerably during the past ten years and the variations seem to find their counterpart in variations in the destitution in the city as shown by the Associated Charities curve. From 1913 to 1917 our average male white cranial capacity centred on 1400 c.c.; in 1918 it was 1330 c.c.; in 1919 it rose to 1440 c.c.; in 1920 it fell to 1400 c.c.; in 1921 it rose to 1470 c.c. and sank in 1922 to 1440 c.c.

We have been able to segregate four types of crania, upon a basis, not of cephalic index or of thickness, but of relation of capacity to linear dimensions. The average cranial capacities of these four types are (α) 1307 c.c., (β) 1383 c.c., (γ) 1449 c.c., (δ) 1501 c.c., the average linear dimensions remaining stationary. The numbers of these types fluctuate from year to year in a surprising and, I think, significant manner, being related to industrial and social conditions in the City. Several characteristic features of the individuals in our dissecting

room population seem to point to a segregation of these cranial capacity types upon social and psychological scales.

It is apparent that cranial capacity affects cranial contour more than cranial linear dimensions.

(B) "Stereoscopic Projection."

The principle of stereoscopic projection is the development of an illusion of three dimensions in an image on the screen. A double lantern is necessary, carrying two gas-filled mazdas each of 1000 watts. By this means two lantern slides of the object, photographed stereoscopically, are projected and superimposed on the screen, the one through a red filter, the other through a green, the filters being complementary in colour. The observer is provided with a spectacle frame in which the lenses are of plain glass, the one being in reality a red filter, the other a green, of precisely the same shades as the filters in the lantern. Thus the "red eye" of the observer sees only the "red image" and the "green eye" sees only the "green image." The result is identical with that of the two unaided eyes looking at an actual object, namely vision in three dimensions. It is not marred by any sensation of colour.

The method is applicable for all objects whether microscopic or gross: it ensures efficient opportunity for every member of a large class and enables them to observe the most minute details at full leisure and obviates the necessity of individual demonstration. Moreover the scheme compels the student's attention by its novelty and by arousing his curiosity. It is time-saving for the instructor. Colour-blind students can utilise the method equally with those of normal vision. From the research standpoint the method provides a new avenue of approach to the principles underlying human vision. It indicates that colour appreciation is a function of the cortex rather than of the retina.

The necessary lantern can be obtained from Bausch and Lomb, 37–38 Hatton Gardens, London, E.C., where the method is being demonstrated. The cameras and lantern slides are procurable from the Section of Industries, Anatomical Laboratory, Western Reserve University, Cleveland, O.

In the perfection of the method for medical teaching and research Dr N. W. Ingalls, Mrs Clark D. Lamberton, and Miss W. M. Kuenzel have played a considerable rôle. I would acknowledge fully my indebtedness to these colleagues.

(C) "Instruments for Skull Measurement."

The instruments comprise a head spanner and a craniostat with Pearson's blocks wrought in aluminium. Both instruments have been described and their instrumental errors computed. The craniostat alone is discussed in a paper with the title "Cranial Capacity and Skull Dimensions," published in the *Journal of Physical Anthropology* in 1923: both instruments are described in an article entitled "The Thickness of the Scalp," and published in the *Journal of Anatomy* for 1924.

The present intention is merely to demonstrate the instruments and to inform the Society that, by the generous assistance afforded by our Trustees, it is now possible to have anatomical and anthropological instruments manufactured by an expert instrument maker at cost and overhead price. We have already supplied many institutions in addition to our own. The Industries Section of the Anatomical Laboratory stands ready to assist in every possible way the furtherance of anatomical and anthropological science by the manufacture of instruments either of standard pattern or of new design.

(12) Mr Ralph Thompson made the following communications:

(A) "A Case of Aberrant Spleen."

This case of aberrant spleen occurred in a married woman, a nullipara, aged 51.

A blood count done by an experienced man was normal.

After injecting the renal pelves with collargol, there was reason to suppose that there might be some lesion of the left kidney, as a hard tender lump in the left lumbar region was found, and this was thought to be associated with the comparatively low situation of the left kidney as displayed by X-rays.

Some slight blurring of the outline of the left renal pelvis was also shown by X-rays.

I cut down on the left kidney and found it to be surrounded by a little fibrous tissue, to be slightly scarred and very freely movable. As I at once came to the conclusion that the swelling was not due to the kidney, I incised the peritoneum and felt a mass on the left side of the vertebral column.

After a partial investigation the swelling was found to be a spleen.

The mass extended from the lower pole of the left kidney to the brim of the true pelvis.

It was, in my recollection, larger at the upper end, and tapered somewhat to its lower end.

I assumed it was spleen, as the peritoneum was seen to be thrown into multitudinous small folds over the mass, just as one is accustomed to see it over the normal spleen.

In addition there were some small vessels entering the spleen exactly in the same way as may be seen occasionally in the normal spleen, when they are entering the capsule detached from the hilum.

I draw attention to the case here, as I cannot find much reference to the matter in our ordinary text books. I do not think it is a case of wandering spleen (Küschenmeister).

There is no doubt that the kidney was movable, and affected by some chronic injury, and further that the organ had become affected internally, as there was pyuria.

I have described the case as I saw it clinically at the operation, but although I put my hand into the region of the normal spleen, I could not feel one.

I did not see any accessory spleens.

There was no mesentery to the displaced spleen, and the arrangement of the vessels gave me the impression of their coming from the systemic circulation, but I do not press this point. I merely give my impression.

I should say that as far as I could see the aberrant spleen was of the normal size.

I think the arrangement of the vessels would rather preclude the view that the organ had undergone displacement after birth.

The spleen has been described as occurring, occasionally, in umbilical herniae.

Such spleens might, of course, be examples of the condition, which I have endeavoured to describe.

Professor Frazer remarked that the spleen was developed in the posterior wall of the omental bursa, and any variation in position would be dependent on varying relations of this, and of its adhesion to the posterior abdominal wall.

(B) "Surgical Anatomy of the Upper Urinary Tract."

Several years ago, in 1913, I drew the attention of this Society to the fact that stones were more often found in the right kidney than in the left.

Four cases of haemorrhage in both renal pelves which were collected from the post-mortem records at Guy's Hospital showed clotted blood in the pelvis of the right kidney, whereas the blood was still liquid in the pelvis of the left kidney.

Apparently tuberculosis and carcinoma affect the right kidney more frequently than the left kidney.

I supposed that the different relations of the kidneys, and ureters on either side was responsible for this retention of blood and accounted for its clotting in the right kidney, and not in the left, since the passage of blood was obstructed to a greater extent on the right side than on the left.

Since this paper was published I have succeeded in getting more evidence that there is more obstruction to the passage of urine on the right side than on the left.

I have seen a case of blood at both orifices of the ureters in the bladder, but that on the right side was clotted, whereas there were frequent spurts of blood on the left.

But the interest of my communication lies in the fact that in my cases of impacted ureteric calculi the large majority are on the right side, and conversely, those patients who have passed stones *per vias naturales* have said that they have had pain on the left side along the course of the ureter.

From a perusal of post-mortem records at Guy's and the London Hospital I am convinced that a large number of stones are formed in the pelvis of the kidney and at an early age, and if this be correct, assuming that they are formed equally on both sides, these later facts are not only of anatomical importance but are also of clinical interest.

I have a patient, a little child who has been operated upon by another surgeon for impacted calculus in the right ureter. She eventually came under my care, and I watched her, as she had stones on both sides. She eventually had left renal colic and passed a stone from her left side, *per vias naturales*.

I wish to draw attention to a point in the anatomy of double ureters, and it is this. In those cases that I have seen the ureters appeared to leave the kidney by a much smaller opening than the single undivided ureter, and it would appear that there is only a very small pelvis, and in fact it seems that the double ureter represents only the upper, and lower parts of the pelvis of the kidney, the main part of the reservoir being absent in these cases of divided ureter.

I have seen cases of double ureter with evidence of urinary obstruction.

Professor BARCLAY-SMITH suggested that differences in the relations of the ascending colon, and of the descending colon to the ureter might account for variations in the passage of urine or calculi through the right or left ureter.

(C) "Transplantation of Rectus for Incontinence."

I hope the Anatomical Society will forgive me for showing some more cases of rectus transplantation for the relief of incontinence which is either due to epispadias, or which results from the opening left after an operation for sewing up an ectopia vesicae, the steps of which have been described by me elsewhere.

I have types of each of these cases here to-day.

The first case will demonstrate that the operation is worth doing, as I think you will agree with me that the girl is a fine specimen of humanity.

In such a case as hers it would have been a pity to put the ureters into the bowel.

The urinary apparatus was separated at an early embryonic age from the intestinal tract, and I do not feel disposed to unite them.

The usual operation was done, no nerves were seen and the wound healed by primary union.

The operation was done a year ago, and at first it seemed that it would be a failure, though she held her water for a longer time than before. I was very fortunate in securing the services of an excellent nurse who took an infinity of trouble with the child, and taught her to hold her water regularly for two hours.

Later she went home and though at first she did well she fell back as the mother could not pay full attention to her. But now that she is back under our care at the hospital, she is holding her water well.

The case has convinced me that careful after-treatment is needful in these cases.

I assume that, a bladder being formed, there is a passive dilation as it fills with water, and it is when the patient desires to pass water that she must be trained to bring the transplanted muscle into action.

By this means a reflex action is taught to the patient, and I hope that the Society will forgive my not mentioning names of those pioneers in nerve surgery who have helped me to realise this point.

The next case is that of a little boy with ectopia vesicae sent to me by Mr Nitch from St Thomas's Hospital. I had sewn up the bladder, but incontinence continued through the epispadiac opening left after the first operation.

I later transplanted the right rectus, and this time a nerve going to the muscle was cut but it was not low down, and apparently has done no harm to the success of the operation so far, for though the boy is very young he is dry at nights for three hours and can hold his water for at least half an hour by day. He will require careful educational treatment.

I have now done six of these cases and one has been undoubtedly a failure, but four of the others have done well, and the case which I reported at the beginning of 1923 can hold her water for three hours in the day, and is never wet when the district nurse, who has taken a great deal of trouble with her, visits the house, but she wets her bed at night.

The sixth case is not completed, but it was a case of ectopia vesicae which I sewed up. There is only a small epispadias left, and I hope to be able to educate the transplanted rectus now, but am doubtful, as the child is rickety, and may not be quite right mentally. I have had no deaths due to the operation. I wonder what is the death roll in the operation of transplanting the ureters or the bladder into the bowel?

I should like to mention a case which fell under my care, as perhaps illustrating the control that a normal rectus may have over control of micturition. I made a suprapubic fistula in an elderly man, who was suffering from an adenoma of the prostate gland. As his kidneys were not in a condition to allow removal of the diseased part, he went home. About six months afterwards I saw him again. He told me that he was able to hold his water for about two hours, and then could pass it voluntarily through the suprapubic opening, and was able to direct the stream into a chamber. The chamber had

to be rather larger than that ordinarily used. This case might occur more frequently if only people would thus train their rectus to assist the comfort of a suprapubic fistula, and it certainly seems to raise most interesting points in connection with the transplantation or use of the rectus in getting control over the flow of urine through a congenital epispadias.

Professor YEATES drew attention to the direction of the nerves passing into the rectus abdominis muscle. The nerves entering the rectus muscle above the umbilicus tend to run upwards, and then turn downwards, while the nerves entering the muscle below the umbilicus course downward, but do not turn upwards. Splitting of the rectus here would be almost certain to divide the nerve.

(13) Mr C. P. G. WAKELEY exhibited a family consisting of a mother and three children all of whom were acrocephalic in a marked degree. The age of the mother was 46. The eldest child was 8, the second 6, and the baby 1½ years. Lantern slides of the X-ray appearances of the skulls were shown; the most marked features were the small amount of frontal bone and the bossing of the internal table of the skull which was very apparent in the X-ray plates.

The Wassermann reaction of all the patients was negative.

They all suffered from a mild form of myopia.

Mr Wakeley said he showed the cases with the object of getting some opinion regarding the cause of the condition and further whether or no any form of treatment might be suggested.

Professor PARSONS said that many of these cases of acrocephaly were associated with irregularity in the closure of the cranial sutures. A premature union of the coronal and lambdoid sutures hindered growth in the length of the skull. This was compensated for by a growth in height which was sometimes accompanied by persistence of the metopic suture.

A difference has been noted in horned, and hornless deer. In the horned the metopic suture remains open, in the hornless it becomes closed.

Professor WINGATE TODD remarked that the shape of the head differed largely according to the manner in which the skull was hafted on to the base. If the facial region is more developed the frontal region will seem to be relatively small. The thickness of the skull varies in different subjects, and influences the time of union of the sutures. After adult life is attained the skull does not increase by more than 1 mm.

Nature requires a certain amount of space for the growth of the brain, and does not mind in what way she obtains this space. In man, and anthropoid apes, there is a departure from the typical mode of union of the sutures, associated with the change in position of the head, and the increase in cranial capacity.

Professor D. WATERSTON (A) read a paper on "The Development of the Hypophysis cerebri in Man and in *Tarsius spectrum*."

He exhibited a series of models to demonstrate successive stages of the development of the hypophysis in man, and also a model of the hypophysis from a *Tarsius* embryo.

The specimens showed that in the human embryo there was not the large outgrowth such as gives origin to the pars tuberalis in *Tarsius*.

(B) Demonstrated a cervical heart from a calf.

Malposition of the heart such as occurred in the present specimen is infrequent, and he was unaware of its occurrence in any animal other than the calf.

A somewhat similar specimen was shown by the late Prof. Wm. Rutherford to his class of Physiology in Edinburgh University a good many years ago, but Professor Waterston had been unable to find any record of the condition of the heart itself.

He was indebted to Mr Young, veterinary surgeon in St Andrew's, for the description of the calf in which the malposition had been found, and for the opportunity of examining the heart. The calf was in other respects well formed, but in the lower part of its neck was a large pulsating mass, which Mr Young at once recognised as the heart.

The cardiac apex appeared to him to be directed towards the mandible, and lay closely beneath it.

The animal was feeble when born; it died within a few hours after birth, before Professor Waterston had had an opportunity of examining it alive. Mr Young removed the heart and sent it to him for examination.

In size and weight the specimen was rather small, weighing 14½ ounces. Its shape was unusual, for the ventricular part formed a long and rather narrow quadrilateral, 3½ inches long and 3¼ inches wide, with no definite apex, but merely a slight indentation on the lower margin, between the right and left borders.

The heart and the vessels attached to it showed many abnormalities.

There was a rather small right vena cava superior, and in addition, a large persistent left vena cava superior, terminating, in the right atrium, by an opening 15 mm. in diameter in the position of the usual orifice of the coronary sinus. This orifice was entirely destitute of any "valve." At the lower and back part of the opening was a minute aperture. This was almost closed by two small thin endocardial folds, which lay flat and flush with the surface of the atrium. This small opening was the mouth of the coronary sinus which received the veins of the heart.

Above and in front of the opening of the left vena cava superior was a large and peculiar patent foramen ovale. The foramen measured 25 mm. vertically, and 20 mm. horizontally. It was largely filled in by a fleshy membrane, which hung in loose folds like a curtain from the upper and posterior margin of the opening. Its lower border, which was fenestrated, was attached to the upper part of the anterior wall, and to the lower margin of the foramen ovale, leaving a funnel-shaped channel below and in front where the two atria communicated with one another. This fold contained muscle fibres.

The opening of the vena cava inferior was high up on the posterior wall, not far below that of the vena cava superior.

The tricuspid valve in the right ventricle was normal, but the valve cusps were short and thickened at their margins.

The columnae carneae were singularly few and small, but there were the usual two papillary muscles, a large anterior and a smaller posterior.

The moderator band was only represented by a thin cord of yellowish coloured tissue, passing from the septal wall to the base of the anterior papillary muscle. There was a similar smaller cord a few millimetres lower down. These two cords were clearly nothing more than the branches of the right limb of the A.-V. bundle.

Four pulmonary veins opened into the left atrium, high up and to the right side on the posterior wall, just above and behind the foramen ovale.

The mitral orifice was normal, but its cusps and especially the aortic cusp were short.

The inner surface of the wall of the left ventricle was unusually smooth, and its septal wall afforded an admirably clear demonstration of the left limb of the A.-V. bundle, streaming downwards on this wall and giving off its branches in the usual manner.

The aortic arch turned to the right instead of to the left, passed in front of the right atrium, and gave off a single large branch towards the head, which divided into two vessels, right and left, of which the larger left one received the termination of a large patent ductus arteriosus. The pulmonary artery was thick walled, and divided as usual into two branches, but just before the division 2 inches above the root, there arose from the right side of the main stem a single very thick-walled short vessel, the above mentioned patent ductus arteriosus, the lumen of which was 5 mm. and the walls 6 mm. in thickness. This vessel terminated as described above in a branch of the aorta.

There were two coronary arteries, normal in their arrangement.

No special note of the position and attachments of the pericardium was made when the specimen was removed.

Mr Young states however that so far as he could ascertain, the heart was enclosed in a normal pericardium. No extension of the pericardium downwards to the diaphragm was noticed.

Discussion. The extraordinary position of the heart is explicable on the view that it had retained its embryonic position close below the mandible, but it is impossible to say whether this malposition was responsible for the occurrence of the numerous vascular abnormalities or whether it in turn was due to them.

The modifications of the interior of the right atrium, especially the absence of any valve of the vena cava inferior, and the peculiar form of the foramen ovale, in association with the persistent left vena cava superior are of some interest.

An explanation must be sought for the occurrence of these multiple defects as a result of a single embryonic lesion.

In the present instance those in the right atrium can be ascribed as due to deficiency of the venous valves of the sinu-atrial opening. Deficiency of the right venous valve would leave open and unrestricted the orifice into the body of the sinus of the left horn of that sinus, which in the human embryo at least opens into the narrow angle between the valves in the floor of the sinu-atrial region. The wide opening would encourage persistence of the left horn and of the left duct of Cuvier, and of the persistent left vena cava superior. Defect of the right venous valve accounts for the absence of a valve of the vena cava inferior, which owes its origin to that structure.

The patent foramen ovale is a large persistent foramen ovale secundum, uncomplicated by the presence of the structures and modifications which produce the limbic bands—in which the left venous valve plays a part. The loose curtain which largely occupies the opening is an extension downwards of the septum atriorum primum, in an attempt to narrow the opening.

The variation of the aorta and the persistent ductus arteriosus do not call for special comment.

NOVEMBER 1925

THE Annual Meeting of the Anatomical Society was held at St Thomas's Hospital, on November 20th, 1925, the President, Professor ELLIOT SMITH, being in the Chair.

(1) Mr ARTHUR HOPWOOD, introduced by the President, showed a skull of neolithic type which was found, together with flint implements, in a gravel pit, covered with chalky material, about 20 feet below the surface. The pit in which it was discovered is on Worm's Heath, Wallingham, Surrey. The skull resembled skulls of a neolithic type from the Gower Peninsula, in South Wales. The principal features presented by the skull were the pronounced brow ridges, the narrow frontal region and the prominent parietal bosses.

Professor PARSONS commented on the great vertical depth of the orbital openings, and stated that in neolithic skulls the openings were not usually so deep. The orbital openings were usually deeper in the female than in the male. He suggested that the great vertical depth of the orbital opening was a sexual characteristic and that on this ground the skull was that of a female. This opinion regarding the sex character of the skull was endorsed by the President. Deep orbital openings were generally found in Nordic skulls, but that the skull was Nordic was most unlikely. If the depth at which the skull was found was 20 feet, it was most improbable that the skull was Saxon.

A full account of the skull will be published later in the *Journal*.

(2) Miss LUCY NAISH demonstrated specimens showing abnormal development of the hallux.

Miss Naish showed the two feet of a baby born (at the eighth month) in the Jessop Hospital, Sheffield. They showed an abnormal position of the hallux on both feet, the hallux being small and set almost at right angles to the rest of the foot. The baby also had:

1. A cleft palate.
2. Slight anencephaly.
3. Abnormal right ventricle.

It survived for 24 hours after birth and the feet were the only parts kept at the post-mortem. One foot (right) had a supernumerary digit and the X-ray photograph of this foot shows five long metatarsals and a short stumpy first metatarsal.

On comparing these feet with those of an embryo of eight weeks (which was shown) it will be seen that in the embryo the hallux normally diverges. In an eleventh-week foetus the hallux is brought into line with the other toes but is still shorter than the second toe. The conclusion is drawn that the development of the hallux was arrested at about the eighth week of development, about the same time as the arrest of development of the palatine arch.

Professor PATTEN said that the left foot was very like that of a gorilla. Another feature of interest was that the metatarsal bones inclined towards the inner side of the foot; the foot of a human embryo at the eighth month also turns inwards. X-ray photographs showed that the metatarsal bone of the great toe was very short and it is possible that the first metacarpal bones may also have been relatively short.

(3) Professor FRANKLIN P. REAGAN, University of California, introduced by Professor HILL, gave a demonstration of the earliest blood vessels of the mammalian embryo studied by means of the injection method.

The youngest mammalian embryo hitherto injected for study is a pig of fourteen somites described by Sabin (1917). The youngest embryo of any kind studied by this method is a chick of nine somites, also described by Sabin. The pig embryo referred to must have had a circulation, and therefore, cardinal veins and a duct of Cuvier, if we may judge from the degree of development of its heart, its optic vesicle, and its brain-flexion. The venous structures mentioned are absent in the figure illustrating it. The injection of Sabin's youngest pig, which possessed fourteen somites, must therefore have been partial only. Sabin's youngest pig embryo in which injection approached completeness had twenty-three somites. It is not to be expected that pig material younger than this will be studied in the near future, as the material presents peculiar difficulties which are very nearly insuperable. Complete injection can scarcely be hoped for if the rupture of the embryonic membranes or blood vessels is a necessary incident of the injection.

In those rodents exhibiting the so-called "inversion" of the germ layers and possessing a highly functional yolk sac which almost completely surrounds the embryo and its amnion, the omphalo-mesenteric vessels may be injected with relative ease while the heart is still beating. Beautiful and complete injections have been made of rat embryos having two and three somites.

Injected embryos are bleached, dehydrated, and finally cleared in a mixture of benzyl benzoate and (in small quantity) oil of wintergreen to which has been added a very slight trace of beechwood creosote. A complete account of this special clearing method should soon appear in the Zoological publications of the University of California.

Injection of these early embryos makes it possible for the first time to obtain a complete study of a vessel situated ventral to the alimentary tract and which, at an early stage, forms the entire proximal part, or artery of origin, of the omphalo-mesenteric artery. It has been designated for some time the subintestinal artery, and has been erroneously regarded as an anastomosis between omphalo-mesenteric and umbilical arteries. Sabin regards it as a true omphalo-mesenteric vessel; the relationships of the vessel in the mouse have been known for a period of years to Professor Arthur Robinson, whose published results appear in the *Text-book of Anatomy* (Cunningham). In the relative figures of this text-book the subintestinal vessel is designated as a ventral aorta of the posterior region. The resolution of this vessel from a yolk sac plexus along with intestinal concrescence has not been observed prior to the present study.

New information has been gained in the study of the primitive anterior cardinal vein (primary head vein plus transverse vein of the first interspace). Coincidently with the backward migration of the heart the anterior cardinal vessel is lengthened by the addition to it of a (dorsal) portion of the primitive duct of Cuvier. Vessels which originally entered the cephalic side of the primitive duct of Cuvier maintain these relationships to it, but inasmuch as the portion of the primitive duct which they enter becomes incorporated into the (definitive) anterior cardinal vein, they are later observed as tributaries of the anterior cardinal vein.

The vessels which primitively enter the cephalic border of the duct of

Cuvier have been figured but not mentioned by Streeter and by Heuser (see *Contributions to Embryology*, Carnegie Institute of Washington, No. 24, Plate II, fig. 22, and No. 77, Plate I, fig. 14). Probably the only attempt to interpret them has been that of Sabin, who designates them as veins of the somatopleure. They play an important part in the history of the mammary and facial veins. Their important early function is the superficial drainage of the branchial region.

The incorporation of the dorsal part of the Cuvierian duct into the anterior cardinal vein takes place by the establishment of new connections of the posterior cardinal vessel with the duct of Cuvier; that is to say, the more inferoventral portions of an originally indifferent and diffuse plexus lying between the upper posterior cardinal (common cardinal of Sabin) region and the duct of Cuvier gradually take charge of the blood from the posterior cardinal vein. With the progressive strengthening of these new connections the upper posterior cardinal (entire common cardinal of Sabin) degenerates. The following observations fail to support the conclusions of Sabin. The primitive duct of Cuvier is not a diffuse plexus lying lateral to the cardinal line for a distance of seven (Sabin, 1915) or less (Sabin, 1917) somites; it is only after the Cuvierian duct has formed as a direct connection between the transverse element of the primitive anterior cardinal vein and the potential venous end of the heart that this diffuse plexus between the posterior cardinal vein and the Cuvierian duct makes its appearance. The Cuvierian duct is not a direct connection between the dorsal aorta and the potential venous end of the heart in all or even in any of the interspaces Nos. 2 and 7 inclusive. It is not even a connection of the posterior or of the "common" cardinal with the omphalomesenteric vein. The anterior cardinal does not increase in length at the expense of the posterior cardinal vein (see Sabin, 1917, p. 80), but at the expense of the duct of Cuvier. The plexus, inferior and dorsal to the duct of Cuvier (described by Sabin, 1917, p. 80, as a plexus "Continuous with the Cardinal System" and giving rise ultimately to the umbilical vein), contains the new connection of the posterior cardinal vein with the duct of Cuvier; that it does not give rise to the umbilical vein is indicated by the fact (Sabin, 1917, Plate I, fig. 1) that the plexus is still present in embryos, which have, in addition to it, a well-established umbilical vein.

The posterior portion of the ventral aorta, instead of ending blindly, drains first into the dorsal-most region of the primitive duct of Cuvier, and then into that portion of the latter vessel which has become a part of the anterior cardinal vein.

In the mammal the posterior cardinal vein cannot be said to arise from diverticula from the dorsal aorta. From very early stages until the full number of somites is reached the neural plexus progresses more rapidly than does the posterior cardinal vein. It can be injected directly from the aortic intersegmentals in stages when corresponding levels of the posterior cardinal vessel cannot be so injected. (Consult also Sabin, 1917, Plate I, fig. 1, and Plate IV, fig. 3.) This observation has been made in injected rat embryos as young as seven somites.

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Professor WILSON congratulated Professor Reagan on the preparation of the superb series of specimens which he had demonstrated to the Society by means of lantern slides. He commented on the description by Professor Reagan of a connection of the ventral aorta with the posterior cardinal vein and the derivation of the supracardinal vein, from the neural [venous] plexus, as being of especial interest. He also alluded to the work of Miss Sabin on the origin of the vena azygos, independently of the posterior cardinal vein.

Professor HILL stated that the origin of the omphalo-mesenteric artery from a subintestinal artery, and its connection with the dorsal aorta was secondary. He also discussed the question as to whether the posterior cardinal vein present in the later embryos arose early, or was a later formation.

Dr WOOLLARD described the method he had employed of injecting pig embryos. He also asked whether Professor Reagan's specimens threw any light on the question of the origin of vessels from plexuses? or as sprouts?

Professor REAGAN said that the posterior cardinal vein possibly arose from fusion of intersegmental arteries. The posterior cardinal vein was not in connection with intersegmental arteries before the establishment of the neural [venous] plexus. It is reasonable to believe that the posterior cardinal vein arises from endothelium.

The pig is incomparably inferior to the rat with regard to the injection of early embryos. In the rat it is unnecessary to use a warm saline solution. The saline solution tends to produce an aggregation of colloidal material.

(4) Dr H. H. WOOLLARD, read a paper on "The Innervation of the Heart," a full account of which is published in the *Journal*, vol. LX, Pt. IV, pp. 345–73.

The PRESIDENT said that Dr Woollard's work had confirmed the researches of Dogiel. His results were obtained by a combination of experimental work with the employment of the *intra vitam* method of staining with methylene blue.

By far the greater number, if not all, of the fibres of the cervical sympathetic are derived from the stellate ganglion. The medullated fibres were not affected by removal of the ganglion.

Professor WILSON commented on the physiological value of the nerve fibres distributed to the coronary vessels. The sympathetic sending dilator fibres to the smaller vessels, and the vagus to the larger blood vessels.

Professor WATERSTON referred to the two theories concerning the contraction of cardiac muscle in relation to a neurogenic or a myogenic system. He asked for an explanation of the association of an increased rate of the heart's beat with contraction of the pupil after excision of the stellate ganglion. He also raised the question of the difficulty of distinguishing the identity of particular nerves in a general network of nerve fibres.

Dr Woollard in reply to Dr Waterston said that his work did not cover the neurogenic, or myogenic control of cardiac contractions. With regard to the cause of acceleration of the heart's action after removal of the stellate ganglion, he did not attach much importance to the result of the experiments. He believed individual fibres did maintain their identity in the nerve plexuses.

(5) Dr Robert Orton Moody, University of California, read a paper on the "Positions of the Abdominal Viscera in Living Subjects."

A Roentgenographic and fluoroscopic study of the abdominal viscera of 1000 healthy university students, an equal number of males and females, no one of them with a history of chronic intestinal trouble or of chronic constipation, has determined some interesting facts that must greatly modify the commonly accepted concept of the topography of these viscera.

A line drawn between the highest points of the iliac crests is used as a base line. The position of the viscera is given with reference to this interiliac line.

The conclusions that may be drawn from this study are as follows:

1. The long stomach with the lowest part of the greater curvature below the interiliac line is found in 81 per cent. of this group of 1000 healthy young adults. This type of stomach with, in some cases, its greater curvature as far as 13 cm., and its lesser curvature, in some cases, 7·5 cm. below the line is normal.

2. The ability of the stomach to function normally does not depend upon its position.

3. The strength of the abdominal muscles has little or no effect on the position of the stomach.

4. The common practice of putting patients to bed with a high diet and certain exercises to change the position of the stomach does not produce its effect by changing the position of the stomach.

5. With the subject in the anatomical position, the pylorus of the stomach is found below the transpyloric plane in over 80 per cent. of this group and below the interiliac line in 5 per cent. of both sexes.

6. The transverse colon with its lowest part in the true pelvis is normal and is seldom or never the cause of gastro-intestinal disturbance.

7. The use of the terms gastroptosis and coloptosis is seldom justifiable.

8. The common position of the lowest part of the caecum is in the true pelvis.

9. The lower border of the liver is found below the interiliac line in over 50 per cent. of males and in over 40 per cent. of females.

10. The form, position and relations of the abdominal viscera are so varied in different individuals and undergo such changes with changes in the position of the subject, that Anatomy should be taught as it is found in the living, not as it is found in the dead.

11. To do such teaching and to carry on research, every Department of Anatomy should be equipped with a good outfit for Roentgenological study and one instructor trained to use it.

Further study now being carried on at University College indicates that in over 50 per cent. of subjects the lowest part of the greater curvature of the *empty* stomach is below the interiliac line and that the stomach assumes the adult position in early childhood.

(6) Professor J. E. Frazer gave a demonstration to show that the precervical sinus is not closed in the way generally supposed. The ectodermal surface of the third arch is not covered in, but remains, roughly, as the skin surface of the neck over the region of the carotid triangle. Placodal areas for nerves IX and X are folded in by the growth of the paraxial mesoderm enclosing the sinus above and behind, thus forming "vesicles" which, at first

connected with the surface by ectodermal ducts, soon lose these connections and disappear. The closing in of the last placode covers in the surface of the fourth arch. The hypoglossal nerve moves forward from behind the last pharyngeal pouch, in such manner that any ectodermal remnants which, in abnormal cases, may connect the surface with the pharynx or other deep structure, will be carried forward with it and must turn over it in order to reach the deep attachment.

The complete paper will be published in the *Journal.*

Professor FAWCETT asked for information regarding the relation of the sternomastoid and platysma muscles to the precervical sinus and if the precervical sinus disappeared, how was the occurrence of branchial fistulae in the neck to be explained.

Professor Frazer stated in reply that cells which seem to form the platysma appeared along the posterior border of the sinus. With regard to branchial fistulae extending high up in the neck, fusion of the second and third arches occurs.

It was difficult to explain the extension of the fistula to the lower part of the neck.

Professor HILL said that in the study of the development of the thymus in marsupials he was under the impression, that the precervical sinus closed partly as the result of a backward growth of the hyoid ridge, and partly by the growth of the ventral ridge. It seemed that in Marsupials the precervical sinus did close, and afterwards disappeared. Placodes were present in most lower mammals, and certainly exercised a control over the nerve cells. They may however form sheath cells not ganglion cells. The cervical vesicle includes the placode connected with the vagus nerve.

Professor WILSON said that the occurrence of cervical vesicles indicates a closure of the deeper part of the sinus, and thus in one sense there must be a distinct fusion.

Professor Frazer in reply said that the placodal area was turned inward. It was possible that the closure of the sinus by the fusion of the second arch with the dorsal ridge might go further in the marsupial than in the human subject.

FEBRUARY 1926

AN Ordinary Meeting of the Society was held in the London Hospital Medical College on February 5th, 1926, the President, Professor ELLIOT SMITH, in the Chair.

(1) Professor J. E. FRAZER showed a reconstruction to illustrate what he considered to be the probable mode of formation of the left common iliac vein. On a previous occasion he had demonstrated the development of a periganglionic plexus (supracardinal system) which is concerned in forming, *inter alia*, the postrenal part of the inferior vena cava, and apparently brings about the preaortic anastomosis through its extension with the nerve elements, in front of the aorta and its secondary connection with the subcardinal vein of its side. It was suggested at the time that a similar mode of connection across the caudal aorta might afford the basis for the transverse pelvic

anastomosis, but no specimen combining exactly the right stage with the necessary injection of the veins was available at the time. The present embryo was in very bad condition, but its veins were injected, and the reconstruction showed the existence of periganglionic vessels, of extension from these in a broken plexus across the caudal aorta, and of connections between this plexus and the more ventral cardinal systems. The specimen evidently filled the gap in the previous series, and provided a definite vascular foundation which could be subsequently enlarged into the transverse anastomosis.

Professor REAGAN said that in his experience gained from the study of these veins in animals by the injection method, the supracardinal veins, adopting McClure's terminology, could be injected in early stages directly from the aortic intersegmental arteries, in stages when the posterior cardinal veins could not.

Professor Frazer in reply said that in the stages of human embryos he had examined the vessels of the periganglionic plexus were in a very rudimentary state. It was difficult to state definitely whether there was a communication of the arteries with the veins.

(2) Dr C. F. EAST showed an abnormality of the occipital bone in which manifestations of an occipital vertebra were present. The description is published in the *Journal*, vol. LIX, Pt. IV, pp. 416–17.

Professor ELLIOT SMITH discussed the question of the anomaly being due to the manifestation of an occipital vertebra. The two halves of the neural arch were developed separately, and usually appeared on the under surface of the occipital bone. An indication of it was however sometimes visible on the cranial aspect, and it was possible that the irritation produced by the hydrocephalus might have produced an exaggeration of this appearance.

(3) Mr L. R. SHORE read a paper on "A Case of Multiple Anomaly of the Phalanges of the Hands in a Girl, aged 15."

Professor BARCLAY-SMITH, Professor WRIGHT, Professor FRAZER, Dr LE GROS CLARK, Mr HUME and Mr WAKELEY joined in the discussion. The general opinion was that the condition, although approximately symmetrical, was pathological, and that impairment of the circulation, as evidenced by the frequent occurrence of chilblains, had interfered with the normal growth of the bones and more especially of the epiphyses.

(4) Professor J. P. HILL gave a demonstration of Embryologia varia (development of *Hapale jacchus*).

He showed a series of lantern slides illustrating the structure and relations to each other and to the uterine wall of two early blastocysts of *Hapale jacchus*, the earliest stage so far observed in the development of any platyrhine monkey. Each ovary showed such a well-marked corpus luteum that two blastocysts were to be expected. In the uterine lumen, however, there was found what appeared at first sight to be a single blastocyst but with two embryonal formations. What apparently happens in this species is as follows. Two blastocysts settle down side by side and become attached to the dorsal and ventral walls of the uterus by their opposite polar areas. Their apposed walls fuse and later on break down with the result that the two embryonal formations come to be enclosed in a common blastocyst wall. Professor Hill also showed lantern slides of a late stage of *Hapale* in which the twin foetuses

were seen to be enclosed in a common chorion but, whilst each foetus was provided with its own discoidal placenta, the umbilical vessels of the two were directly connected by anastomoses.

Professor FRAZER enquired whether the platyrhine monkeys could be divided into several groups with regard to the relations of the cytotrophoblast, and also whether Professor Hill regarded the second specimen of *Hapale* as resulting from the division of a single blastoderm.

Professor Hill replying to the question of the variations in placentation among platyrhine monkeys said that the fundamental plan was the same in different groups. Villi are present, but they tend to become so connected as to form a network. Possibly there were intermediate types, but he had not observed continuous grades. In the howling monkeys there is a single discoidal placenta. In *Hapale* there is a double placenta and the blastocysts are attached to the two opposite walls of the uterus. Fusion of the median walls takes place and the partition thus formed afterwards breaks down. The trophoblast is formed in relation to the attached area. With a single blastocyst there may be two embryos, and two umbilical cords. He considered that the form of placentation might be found useful in determining the relation of different types, more particularly in certain orders such as the Primates. The placenta of the flying squirrel was however practically indistinguishable from that of a monkey.

(5) Dr LE GROS CLARK, read a paper on "The Mammalian Oculomotor Nucleus," which is published in full in the *Journal*, vol. LX, Pt. IV, pp. 426–48.

Dr MANN considered that the current views with regard to the function of the cell groups in the oculomotor nuclei had received general credence on insufficient grounds. It is doubtful what the true function of the Edinger-Westphal nucleus is. The median nuclei appeared to be developed as a part of the main nucleus of the third nerve. It is doubtful whether there is any reaction of the pupil to light in the hedgehog or not.

Dr WOOLLARD said that Winckler in conjunction with Magnus at Utrecht had obtained experimental proof that the nucleus of Perlia was definitely concerned with convergence of the eyes.

He however had failed to obtain any evidence that the so-called nucleus of Edinger-Westphal had anything to do with the control of the pupil.

Dr Woollard also mentioned that Barrington of University College had shown him a lesion in the mid-brain of a cat which was situated on the lateral side of the central canal just outside the mesencephalic root of the fifth. This lesion, which was far away from the position of the Edinger-Westphal nucleus, was accompanied by paralysis of the pupil, the pupils being fixed in dilatation.

He disagreed with the opinion that the muscles in the oculomotor nucleus could not be definitely localised, since the precise localisation of muscles had been found to hold in all motor cranial nerve nuclei examined from this point of view, as, for example, the hypoglossal.

Professor ELLIOT SMITH remarked that the lateral rectus and superior oblique muscle were undoubtedly represented by definite groups of nerve cells, the nuclei of the IVth and VIth cranial nerves. In the cat the visual fields overlap and it is able to converge the eyes. The late Professor Hunter expected to find paramedial nuclei in *Nycticebus*, but apparently did not do so. The function of the Edinger-Westphal nucleus was doubtful, possibly

a nucleus of accommodation. A nucleus posterior to it has been shown to be the nucleus controlling the action of the pupil.

Dr Le Gros Clark replied that he believed the Edinger-Westphal nucleus to be a part of the oculomotor nucleus. In the cat the nucleus of convergence is very well developed. In the lemur it is practically absent. He considered that the central position of the cells was not essential to the act of convergence of the eyes but that the cells were pushed inwards towards the median plane by the growth of the more lateral groups of cells.

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